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NITROGEN EXCESS IN NORTH AMERICAN ECOSYSTEMS: PREDISPOSING FACTORS, ECOSYSTEM RESPONSES, AND MANAGEMENT STRATEGIES

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Abstract. Most forests in North America remain nitrogen limited, although recent studies have identified forested areas that exhibit symptoms of N excess, analogous to overfertilization of arable land. Nitrogen excess in watersheds is detrimental because of disruptions in plant/soil nutrient relations, increased soil acidification and aluminum mobility, increased emissions of nitrogenous greenhouse gases from soil, reduced methane consumption in soil, decreased water quality, toxic effects on freshwater biota, and eutrophication of coastal marine waters. Elevated nitrate (NO_3^-) loss to groundwater or surface waters is the primary symptom of N excess. Additional symptoms include increasing N concentrations and higher N:nutrient ratios in foliage (i.e., N:Mg, N:P), foliar accumulation of amino acids or NO_3^-, and low soil C:N ratios. Recent nitrogen-fertilization studies in New England and Europe provide preliminary evidence that some forests receiving chronic N inputs may decline in productivity and experience greater mortality. Long-term fertilization at Mount Ascutney, Vermont, suggests that declining and slow N-cycling coniferous stands may be replaced by fast-growing and fast N-cycling deciduous forests.

Symptoms of N saturation are particularly severe in high-elevation, nonaggrading spruce–fir ecosystems in the Appalachian Mountains and in eastern hardwood watersheds at the Fernow Experimental Forest near Parsons, West Virginia. In the Los Angeles Air Basin, mixed conifer forests and chaparral watersheds with high smog exposure are N saturated and exhibit the highest streamwater NO_3^- concentrations for wildlands in North America. High-elevation alpine watersheds in the Colorado Front Range and a deciduous forest in Ontario, Canada, are N saturated, although N deposition is moderate ($\sim 8\ kg \cdot ha^{-1} \cdot yr^{-1}$). In contrast, the Harvard Forest hardwood stand in Massachusetts has absorbed >900 kg N/ha during 8 yr of N amendment studies without significant NO_3^- leaching, illustrating that ecosystems vary widely in the capacity to retain N inputs.

Overly mature forests with high N deposition, high soil N stores, and low soil C:N ratios are prone to N saturation and NO_3^- leaching. Additional characteristics favoring low N retention capacity include a short growing season (reduced plant N demand) and reduced contact time between drainage water and soil (i.e., porous coarse-textured soils, exposed bedrock or talus). Temporal patterns of hydrologic fluxes interact with biotic uptake and internal cycling patterns in determining ecosystem N retention. Soils are the largest storage pool for N inputs, although vegetation uptake is also important. Recent studies indicate that nitrification may be widespread in undisturbed ecosystems, and that microbial assimilation of NO_3^- may be a significant N retention mechanism, contrary to previous assumptions. Further studies are needed to elucidate the sites, forms, and mechanisms of N retention and incorporation into soil organic matter, and to test potential management options for mitigating N losses from forests. Implementation of intensive management practices in N-saturated ecosystems may only be feasible in high-priority areas and on a limited scale. Reduction of N emissions would be a preferable solution, although major reductions in the near future are unlikely in many areas due to economic, energy-use, policy, and demographic considerations.

Key words: atmospheric nitrogen deposition; eutrophication; forest ecosystems; nitrate leaching; nitrogen cycling; nitrogen saturation; soil acidification.

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Introduction

Human alteration of the nitrogen cycle has increased dramatically in recent years (Vitousek et al. 1997*b*). Increased N availability is having unwanted and unintended consequences in some terrestrial, freshwater, and marine ecosystems across the globe (Vitousek et al. 1997*a*). Nitrogen is unique among nutrients not only as a widespread air, soil, and water pollutant, but also as the predominant limiting nutrient in terrestrial ecosystems throughout much of the world. Other major nutrients (P, S, K, Ca, Mg, Mn) originate primarily from soil minerals and can accumulate to a substantial degree on soil exchange complexes. Nitrogen, however, originates from the atmosphere as an inert gas, is intimately tied to organic matter, and rarely accumulates to a significant degree on soil exchange complexes. Although soils are the largest N pool in forest ecosystems (usually exceeding 80% of total ecosystem N capital), most soil N is in organic forms unavailable for plant uptake. However, recent studies report that plant uptake of simple organic N is greater than previously thought, at least in some ecosystems (Kaye and Hart 1997). In temperate forests, available soil N pools are typically very small in relation to the N budget and must turn over several times per year to meet N demand by trees. Thus, it is not surprising that N deficiency is common in forest ecosystems.

Although most temperate forests remain N limited, in an increasing number of forests N limitation has been reversed so that N availability is in excess of biotic and abiotic N retention capacity (Stoddard 1994, Aber et al. 1995, Dise and Wright 1995). The altered N status of these forests is usually attributed to chronic N deposition, although disturbance, land use and management history, stand-successional trends, and climate changes (Mitchell et al. 1996*a*) also affect N cycling and the balance of N inputs and losses from watersheds. Excess N is exported from forests primarily as nitrate (NO_3^-) in groundwater and streamwater and secondarily as gaseous emissions from soil. The syndrome of ecosystem responses to chronic N inputs has been formally described as the nitrogen saturation hypothesis (Aber et al. 1989). Nitrogen saturation has been defined in several ways (Ågren and Bosatta 1988, Aber et al. 1989, Aber 1992, Stoddard 1994, Binkley and Högberg 1997), but can be considered most generally as the long-term removal of N limitations on biotic activity, accompanied by a decrease in N retention capacity (Magill et al. 1996). Nitrogen saturation of watersheds has contributed to environmental problems such as reduced drinking water quality, nitrate-induced toxic effects on freshwater biota, eutrophication of estuaries, disruptions in nutrient cycling, increased soil acidification and aluminum mobility, increased emissions from soil of nitrogenous greenhouse trace gases, reduction of methane consumption in soil, and forest decline and reduced productivity.

The N saturation conceptual model predicts that changes in nitrification, NO_3^- leaching, trace gas fluxes, and forest production are nonlinear in response to continuing increases in N deposition, mineralization, and overall N availability. Nitrogen saturation is hypothesized to progress through four stages as N inputs accrue in the forest (Aber et al. 1989). Stage 0 is described as the typical condition of N limitation. Stage 1 occurs when N concentrations in foliage and possibly tree production increase, and brief periods of N losses from the system are temporarily amplified. In stage 2, N losses from the forest are sustained and nitrification increases. In most instances, reports of N-saturated forests refer to stage 2 of the Aber model (Fig. 1a). In stage 3, chronic N inputs lead to forest decline or decreased productivity. At least four long-term fertilization studies, using realistic low levels of N fertilization, demonstrate that chronic N inputs can cause reduced wood production or greater mortality (Aber et al. 1995, Tamm et al. 1995, Magill et al. 1996, 1997, McNulty et al. 1996). Stoddard (1994) defined a set of progressive stages for watershed N saturation analogous to the terrestrial N saturation model. Some natural systems with little human disturbance and low anthropogenic N inputs exhibit the symptoms of N saturation, e.g., Denali National Park in central Alaska (Stottlemyer 1992), and forests on gravelly soils with a major alder N_2-fixing component (Van Miegroet et al. 1992*a*).

This paper reviews the phenomenon of N excess in North American ecosystems by summarizing data from case studies. We will focus on N-saturated ecosystems, but we do not wish to convey the impression that all forests will become N saturated or that N saturation is as yet a widespread problem. Our major objectives are to describe the geographic extent and factors predisposing terrestrial ecosystems to N saturation; to compare the responses of ecosystems to N deposition in widely different climates, vegetation types, and levels of N inputs; to discuss management strategies for reducing N losses from watersheds and undesirable environmental impacts of excess N; and to outline the effects of N loss from watersheds on downstream estuaries and coastal marine systems. The organization of this review is outlined in Fig. 2.

Geographic Extent of N-saturated Ecosystems in North America

Many reports of N-saturated forests in Europe and North America (Table 1) have confirmed the major tenets of ecosystem responses to chronic N inputs as postulated in the N saturation hypothesis (Fig. 1a). Although S emissions have decreased in developed countries, N emissions are increasing in many areas of the world (Lövblad et al. 1992, Galloway et al. 1994, Galloway 1995, Lynch et al. 1995), suggesting that N sat-

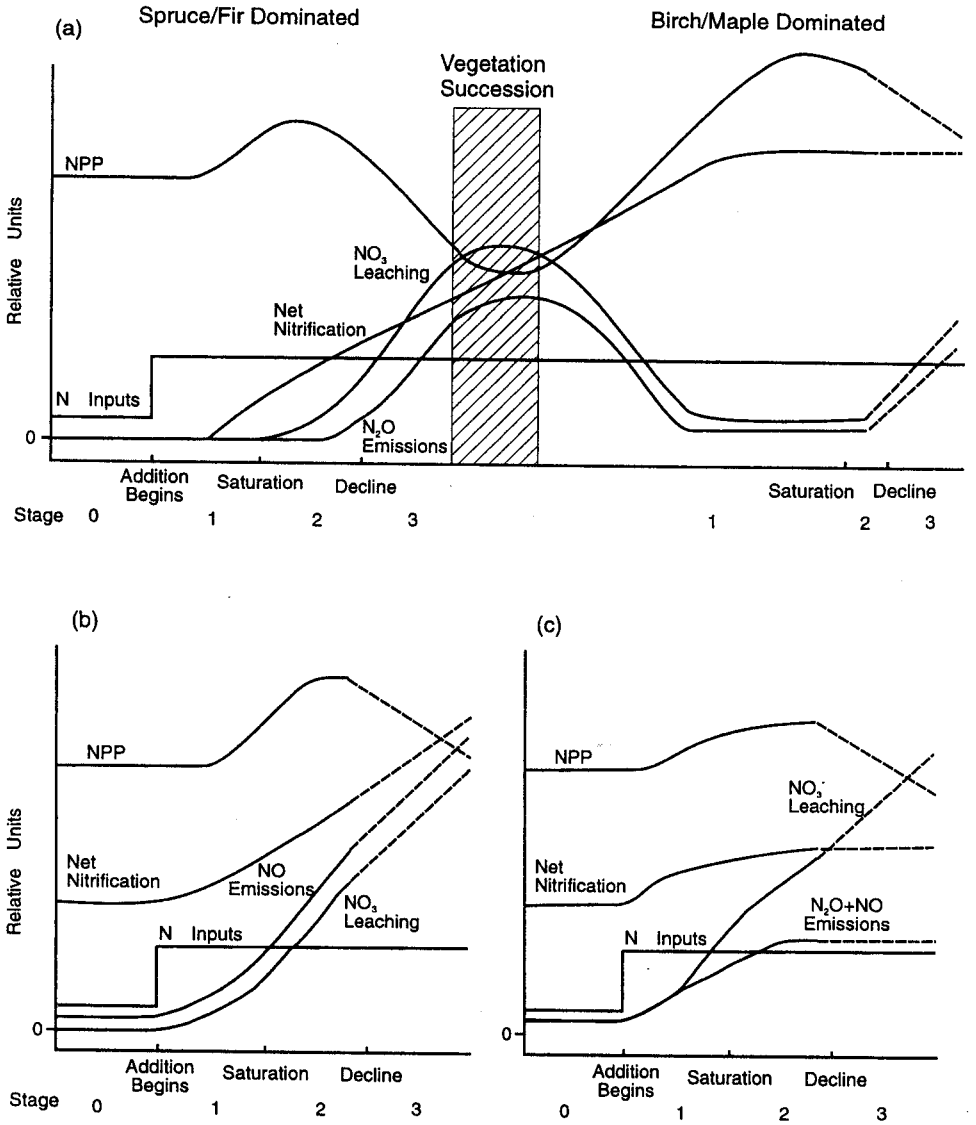

FIG. 1. Hypothesized time course or conceptual model of forest ecosystem responses to chronic N additions: (a) as proposed by Aber et al. (1989, 1995) based on data from forests in New England and in recent N fertilization studies (McNulty et al. 1996), and (b) as proposed for western xeric forests based on recent data (Riggan et al. 1985, Fenn et al. 1996, Kiefer and Fenn 1997) and environmental, edaphic, climatic, and N-processing characteristics of xeric ecosystems in the Los Angeles Air Basin and throughout California. (c) Hypothesized response curves for western high-elevation alpine ecosystems based on data and modeling results from the Colorado Front Range (Baron et al. 1994, Williams et al. 1996*a*, *b*). Dashed portions of lines depict unobtainable ecosystem trends near and beyond stand decline. However, NO_3^- leaching and trace gas emissions from soil may increase further with even higher N deposition. Positions of the lines along the *y*-axes are diagrammatic and are not intended to show relative rates of one process to another.

uration of terrestrial ecosystems may become more common. The northeastern and eastern central regions of the United States receive the greatest atmospheric N deposition in North America. Stoddard (1994) concluded that geographic patterns of N deposition followed the patterns of watershed N loss in the northeastern United States, with the greatest N deposition and watershed losses in the Adirondack and Catskill mountains in New York and little N loss in Maine, where N deposition is about 50% lower. The large number of urban watersheds clustered in the northeastern and central United States account for the large N inputs in the region (Puckett 1995). In contrast, across most of the western and parts of the southern United States, available data suggest that N deposition is substantially elevated only downwind of isolated urban centers. Because urban centers are less aggregated in the western United States, extensive forested regions are not exposed to highly elevated N deposition, with the exception of forests in southern California, the southwestern

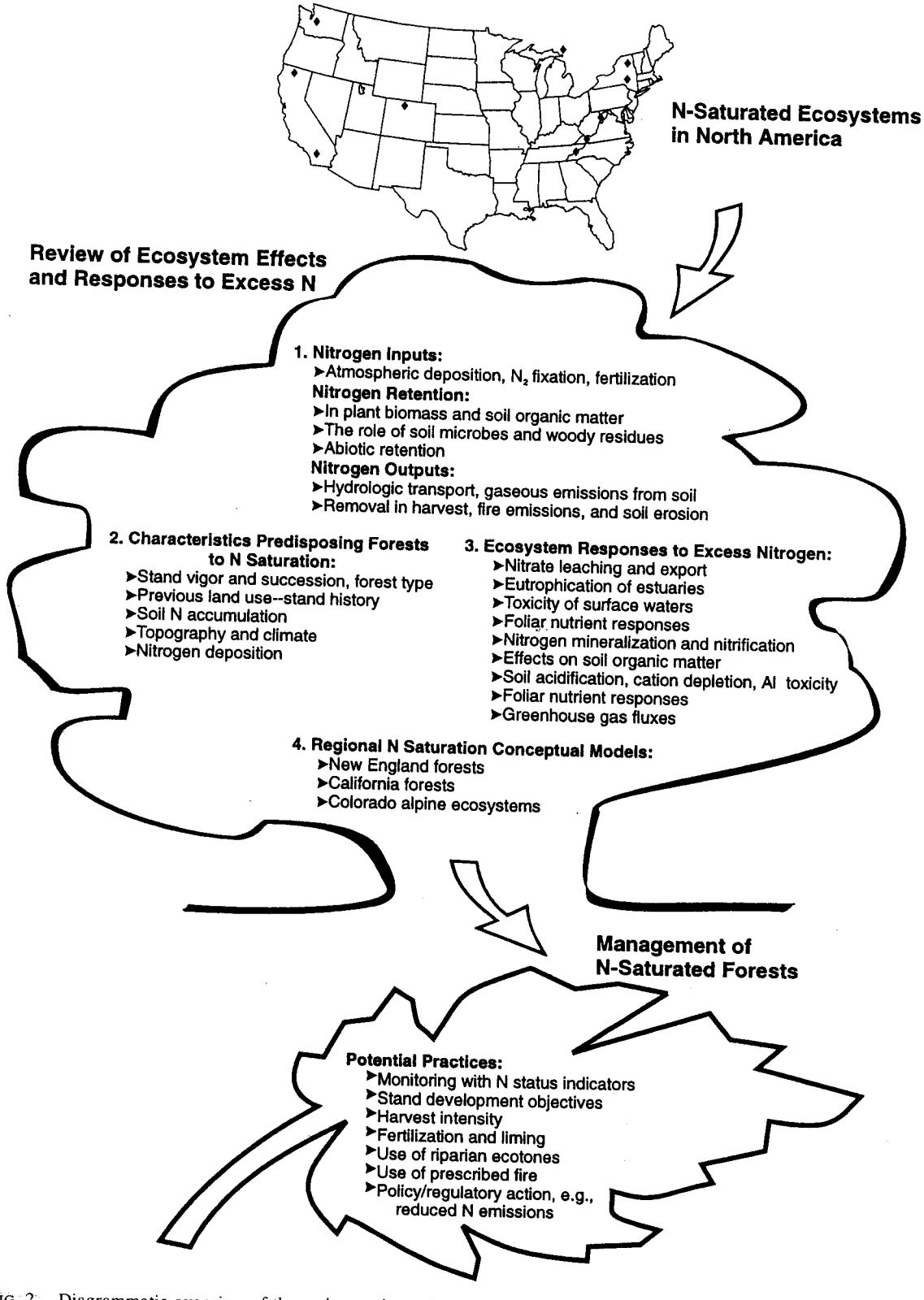

FIG. 2. Diagrammatic overview of the major sections of this review of N excess in North America. The N-saturated sites shown on the map are listed and described in Table 1.

TABLE 1. Nitrogen-saturated forests in North America including estimated N inputs and outputs.

Location	Forest type	Elevation (m)	N input ($kg \cdot ha^{-1} \cdot yr^{-1}$)	N output ($kg \cdot ha^{-1} \cdot yr^{-1}$)	Reference
Adirondack Mts., northeastern New York	northern hardwoods or hardwood/conifer mix	396–661	9.3†	Stage 1 N loss‡	Driscoll and Van Dreason (1993)
Catskill Mts., southeastern New York	mainly hardwood; some eastern hemlock	335–675	10.2†	Stage 1 and 2 N loss‡	Stoddard (1994)
Turkey Lakes Watershed, Ontario, Canada	sugar maple and yellow birch	350–400	7.0–7.7 (as throughfall)	17.9–23.6	Foster et al. (1989*a*), Johnson and Lindberg (1992)
Whitetop Mt., southwestern Virginia	red spruce	1650	32§	47§	Joslin and Wolfe (1992), Joslin et al. (1992)
Fernow, West Virginia	mixed hardwood	735–870	15–20	6.1	Gilliam et al. (1996), Peterjohn et al. (1996)
Great Smoky Mts. National Park, Tennessee	American beech	1600	3.1‖	2.9	Johnson and Lindberg (1992)
Great Smoky Mts. National Park, Becking Site, North Carolina	red spruce	1800	10.3‖	19.2	Johnson et al. (1991)
Great Smoky Mts. National Park, Tower Site, North Carolina	red spruce	1740	26.6	20.3	Johnson et al. (1991)
Front Range, Colorado	alpine tundra, subalpine conifer	3000–4000	7.5–8.0	7.5	Williams et al. (1996*a*)
San Dimas, San Gabriel Mts., southern California	chaparral and grasslands	580–1080	23.3¶	0.04–19.4	Riggan et al. (1985)
Camp Paivika, San Bernardino Mts., southern california	mixed conifer	1600	30	7–26#	Fenn et al. (1996)
Klamath Mts., northern California	western coniferous	NA	Mainly geologic††	NA††	Dahlgren (1994)
Thompson Forest, Cascade Mts., Washington	red alder	220	4.7 plus >100 as N_2 fixation	38.9	Johnson and Lindberg (1992)

† Estimated total N deposition from wet deposition data is from Driscoll et al. (1991) for the Adirondacks, and from Stoddard and Murdoch (1991) for the Catskills. Total deposition was estimated based on the wet deposition/total N deposition ratio (0.56) at Huntington Forest in the Adirondacks (Johnson and Lindberg 1992). Nitrogen deposition can be higher in some areas, especially at high-elevation sites such as Whiteface Mountain (15.9 $kg \cdot ha^{-1} \cdot yr^{-1}$; Johnson and Lindberg 1992).

‡ Stage 1 and 2 of N loss according to the watershed conceptual model of Stoddard (1994). Nitrogen discharge ($kg \cdot ha^{-1} \cdot yr^{-1}$) data are not available; only streamwater NO_3^- concentration trend data were collected.

§ Values appear high compared to other sites, especially N leaching losses. Joslin and Wolfe (1992) concede that "there is considerable uncertainty associated with the estimates of atmospheric deposition and leaching fluxes." However, elevated NO_3^- concentrations in soil solution, and lack of a growth response to N fertilization (Joslin and Wolfe 1994) support the hypothesis that the forest at Whitetop Mountain is N saturated.

‖ Estimated total N deposition from throughfall data. Total deposition was estimated based on the throughfall/total N deposition ratio (0.56) from the nearby Smokies Tower site (Johnson and Lindberg 1992).

¶ Annual throughfall deposition to the chaparral ecosystem.

Nitrogen output is from unpublished streamwater data (M. E. Fenn and M. A. Poth). The low value represents a year of average precipitation, and the high value is for 1995, when precipitation was nearly double the long-term average. Nitrogen output includes N export in streamwater and to groundwater.

†† Annual input and output data are not known, although N deposition in this forest is probably typical for much of the rural western United States (2–3 $kg\ N \cdot ha^{-1} \cdot yr^{-1}$; Young et al. 1988). Excess N is from weathering of ammonium in mica schist bedrock. The ammonium was rapidly nitrified, leading to high NO_3^- concentrations in soil solution (Dahlgren 1994).

Sierra Nevada in central California, the Front Range in northern Colorado, and possibly downwind of other expanding urban areas. However, over large areas of North America and Europe, N deposition is significantly higher than levels measured in pristine areas (Weathers et al. 1988, Bormann et al. 1989, Zöttl 1990). Nitrogen deposition is believed to increase plant growth in these areas (Kauppi et al. 1992, Eriksson and Johansson 1993).

Nitrogen-saturated forests and watersheds have been reported in southern California and along the Colorado Front Range, where N deposition from nearby urban areas and from agriculture has contributed to N levels that exceed ecosystem N retention capacity. Phytoplankton communities in the ultra-oligotrophic Lake Tahoe, on the California–Nevada border, have changed from colimitation by N and P to P limitation, presumably because of atmospheric N deposition (Jassby et al. 1994). Annual N deposition inputs (6–11 $kg \cdot ha^{-1} \cdot yr^{-1}$ as throughfall) in the southwestern Sierra Nevada (Chorover et al. 1994) are similar to N storage (4–10 $kg \cdot ha^{-1} \cdot yr^{-1}$) in the vegetation increment of

western forests (in woody biomass; Johnson 1992), suggesting that current N deposition rates may be near the assimilation capacity of the overstory vegetation. However, growth increases caused by N deposition are also expected to increase N uptake and storage in vegetation and litter (Nilsson and Wiklund 1995). Most urban centers in the western United States are adjacent to forest lands, and ongoing urban expansion is likely to result in greater N deposition, with increasing potential for N saturation of forests near urban source areas (Böhm 1992; e.g., Salt Lake City, Seattle, Tucson, Denver, central and southern California), unless improved emission controls offset the effects of increased population.

In Canada, the highest N deposition and NO_3^- concentrations in surface waters occur in south-central Ontario and southwestern Quebec. The highest level of N deposition (13 kg $N \cdot ha^{-1} \cdot yr^{-1}$) is moderate compared to high deposition areas in Europe and the United States (Jeffries 1995). Lac Laflamme in Quebec and Turkey Lakes in Ontario exhibit NO_3^- export patterns of stages 1 and 2, respectively, of watershed N saturation (sensu Stoddard 1994). Moderate NO_3^- export to lakes occurs in many watersheds in southeastern Canada. In regions with the lowest N deposition, such as Newfoundland and Labrador, NO_3^- concentrations in lakes are generally near zero (Jeffries 1995).

Nitrogen Inputs, Retention, and Outputs

In simple terms, the degree of N saturation of a forest stand is determined by the balance between inputs of available N (e.g., from N mineralization and atmospheric deposition) and the N retention capacity of the plant–soil–microbial system. A number of watershed N amendment experiments in North America have demonstrated the limited capacity of many forested watersheds to retain all of the added N (Adams et al. 1993, Kahl et al. 1993, Norton et al. 1994, Gilliam et al. 1996). Although it is clear that biotic uptake of N is a major sink for available soil N, as evidenced by the seasonality of N loss from watersheds, few studies (Davidson et al. 1990, 1992, Zak et al. 1990, Nadelhoffer et al. 1995) provide quantitative information on the relative importance of soil microbial N retention, abiotic retention, and plant uptake of N. Ecosystem retention of chronic N inputs is governed by N pools and processes operating over a wide range of pool sizes and timescales. For example, microbial biomass is a small N pool, but assimilation and turnover of N can be very rapid (hours). In contrast, soil organic N pools are large, but dominated by fractions with slow decomposition (years, decades, or centuries) and slow N mineralization rates.

Nitrogen inputs

The principal N inputs to forest ecosystems include atmospheric wet and dry deposition, symbiotic N_2 fixation (e.g., *Rhizobium* and *Frankia* bacteria forming root nodules), and fertilization. Associative N_2 fixation by microbes in the rhizosphere (Li et al. 1992, Bormann et al. 1993*a*), N_2 fixation by free-living soil organisms, and N_2 fixation by cyanolichens in the canopy (Sollins et al. 1980) may be important N sources in some ecosystems. In the Hubbard Brook sandbox ecosystem study, it was reported that microorganisms associated with rhizospheres of red pine (*Pinus resinosa* Ait.) and pitch pine (*Pinus rigida* Mill.) fixed ~50 kg $N \cdot ha^{-1} \cdot yr^{-1}$ (Bormann et al. 1993*a*). Cyanobacteria in microbiotic soil crusts (composed of nonvascular plants and microbes) are important sources of fixed N in some arid and semiarid ecosystems (Evans and Ehleringer 1993, Eldridge and Greene 1994). Rare geologic sources of excess N can also lead to soil acidification, cation leaching, and high NO_3^- and aluminum (Al^{3+}) concentrations in soil solution (Dahlgren 1994).

Retention in plant biomass

Plant uptake of N is an important retention mechanism (Johnson 1992, Emmett et al. 1993, Edmonds et al. 1995), although N retention by vegetation is generally less than soil storage. Plant N uptake depends on the vigor and successional stage of the forest. Younger trees have less N storage reserves, depend more on the soil for N, and are more effective at retaining N in plant biomass than are older trees. Plant uptake was still an important N retention mechanism, however, in an old-growth, uneven-aged forest in Washington state (Edmonds et al. 1995). In some forests, N retention in understory vegetation can be significant relative to the overstory (Melin et al. 1983, Mugasha and Pluth 1994, Preston and Mead 1994, Buchmann et al. 1996).

Retention in soil

Forest fertilization studies have shown that litter and soils are major N sinks (Heilman and Gessel 1963, Mead and Pritchett 1975, Miller et al. 1976, Melin et al. 1983, Raison et al. 1990). Soil organic matter is the largest reservoir of N in forest ecosystems, usually exceeding 85% of total ecosystem capital (Cole and Rapp 1981). In a survey of 29 N fertilization studies, an average of 28% of the added N was recovered in the vegetation compared to 39% in the soil (Johnson 1992). In the ^{15}N tracer studies summarized in Table 2, 6–33% of the labeled NH_4^+ was recovered in vegetation and 30–87% was retained in soil. Of the labeled NO_3^- applied to forest ecosystems, 4–37% was recovered in vegetation and 19–86% in soil, demonstrating the greater retention capacity of soil.

Young soils or soils where organic C and N pools have been reduced by disturbance (e.g., fire or agricultural cropping) actively accumulate organic matter and N. Nitrogen retention in these systems should be near maximum. Older soils that have accumulated large amounts of N in the mineral soil and forest floor are prone to leach high levels of NO_3^-. Nitrogen storage in litter and humus may be high in forests with chronic

TABLE 2. Distribution and fate of ^{15}N applied to forest ecosystems.

Location	Vegetation, stand age, and sampling time	Percentage retained of added ^{15}N			Reference
		Vegetation	Soil	Leaching	
Labeled ammonium applied					
Maine	mixed northern hardwoods, ~40 yr old, 1 yr	10	70 (forest floor and 0–5 cm soil)		Nadelhoffer et al. (1993)
California	mixed conifer, 10 yr old, 16 mo	plant uptake prevented	47 (40 in SOM, 4 in microbial biomass, 3 in acid extract)		Hart et al. (1993)
Florida	slash pine,† 11 yr old	25	30 (21 in soil, 9 in litter)		Mead and Pritchett (1975)
British Columbia	lodgepole pine, 11 yr old (after 1 season)	8 (5 in trees, 3 in understory)	87 (top 30 cm)		Preston and Mead (1994)
British Columbia	lodgepole pine, 11 yr old (after 8 seasons)	18 (16 in trees, 2 in understory)	43 (5 in litter, 38 in top 30 cm soil)		Preston and Mead (1994)
Germany	Norway spruce, 15 yr old, 8 mo	14‡	71 (63 in organic horizon, 8 in mineral soil)	16	Buchmann et al. (1996)
Sweden	Scots pine, 90 yr old, 1 yr	6	57 (29 in litter and humus, 28 in mineral soil)		Nömmik and Popovic (1971)
Sweden	Scots pine, 120–140 yr old, 2 yr	30 (22 in tree, 8 in shrub layer)	52 (22 in litter and humus, 30 in 0–30 cm soil)	18 (estimated by difference)	Melin et al. (1983)
The Netherlands	Douglas-fir, 35 yr old, high N deposition, 21 mo	29	37	33	Koopmans et al. (1996)
The Netherlands	Douglas-fir, 35 yr old, low N deposition, 21 mo	33	46	2	Koopmans et al. (1996)
The Netherlands	Scots pine, 45 yr old, high N deposition, 21 mo	17	37	17	Koopmans et al. (1996)
The Netherlands	Scots pine, 45 yr old, low N deposition, 21 mo	10	65	10	Koopmans et al. (1996)
Labeled nitrate applied					
Maine	Mixed northern hardwoods, ~40 yr old (28 kg $N \cdot ha^{-1} \cdot yr^{-1}$ added), values are annual means (4 yr)	11	86 (15 in litter and top 5 cm soil, 71 in deeper soil)	3§	Nadelhoffer et al. (1995)
Maine	mixed northern hardwoods, ~40 yr old (56 kg $N \cdot ha^{-1} \cdot yr^{-1}$ added), values are annual means (4 yr)	12	81 (11 in litter and top 5 cm soil)	7§	Nadelhoffer et al. (1995)
British Columbia	lodgepole pine, 11 yr old (after 1 season)	5 (2 in trees, 3 in understory)	39 (in top 30 cm soil)		Preston and Mead (1994)
British Columbia	lodgepole pine, 11 yr old (after 8 seasons)	7 (5 in trees, 2 in understory)	21 (3 in litter, 18 in top 30 cm soil)		Preston and Mead (1994)
Germany	Norway spruce 15 yr old, 8 mo	25‡	63 (46 in organic horizon, 17 in mineral soil)	16	Buchmann et al. (1996)
Sweden	Scots pine, 90 yr old, 1 yr	4	19 (9 in litter and humus, 10 in mineral soil)		Nömmik and Popovic (1971)

TABLE 2. Continued.

Location	Vegetation, stand age, and sampling time	Percentage retained of added ^{15}N			Reference
		Vegetation	Soil	Leaching	
Sweden	Scots pine, 120–140 yr old, 2 yr	37 (28 in tree, 9 in shrub layer)	39 (13 in litter and humus, 26 in 0–30 cm soil)	24 (estimated by difference)	Melin et al. (1983)

† *Pinus elliottii* var. *elliottii* Engelm.

‡ In the $^{15}NH_4^+$ treatment, 3.4% of the ^{15}N was retained in the overstory and 9.1% in the understory aboveground biomass, and 1.0% in roots. In the $^{15}NO_3^-$ treatment, 6.5% of the ^{15}N was retained in the aboveground biomass of the overstory, 14.8% in that of the understory, and 3.5% in roots. Retention of ^{15}N was greater in the understory despite a much lower biomass in the understory (Buchmann et al. 1996).

§ Nitrogen retained in deeper soil layers was determined by difference. Leaching loss data are from ecosystem budgets (Magill et al. 1996).

N deposition because of N-induced retardation of decomposition (Berg et al. 1987, 1995). However, NO_3^- leaching can be high as a result of the large organic N pool size, notwithstanding the retarded decomposition rates (Foster et al. 1989*b*).

Microbial N retention.—The prevailing paradigm is that little NH_4^+ is nitrified in N-limited forests because plants outcompete nitrifiers for NH_4^+. Some have questioned this concept (Davidson et al. 1992, Johnson 1992, Kaye and Hart 1997), and have suggested that microbial assimilation of NO_3^- is important even in N-limited systems. Stark and Hart (1996) reported high gross nitrification rates in 11 undisturbed forest ecosystems in New Mexico and Oregon, and found microbial assimilation of NO_3^- to be an important N retention mechanism. Net nitrification rates (usually the only rate measured) poorly predicted gross rates because the soil microbial communities had the capacity to assimilate almost all of the NO_3^- produced (Davidson et al. 1992, Stark and Hart 1996).

In a northern hardwood forest in Michigan, microbial immobilization of N in early spring was a larger sink than plant uptake, and lessened the potential for N losses from the system (Zak et al. 1990). Microbial processing of N can be significant in the dormant season, especially under snow cover (Brooks et al. 1996, Williams et al. 1996*b*). Microbial N assimilation in forest soils appears to be limited by available soil C (Foster et al. 1980, Bååth et al. 1981, Flanagan and Van Cleve 1983). Stark and Hart (1996) investigated the C-limitation hypothesis, and concluded that in the 11 forest ecosystems they studied, sufficient C was fixed to sustain the high rates of microbial NO_3^- assimilation measured throughout the growing season. Cheng et al. (1996) found that microbial respiration was not limited by available carbon in the rhizoplane and rhizosphere. Nitrogen has also been shown to limit microbial biomass production (Wang and Bakken 1997). Microbial N retention in the rhizosphere may be a major N sink, with mycorrhizal fungi playing an important role in N retention (Aber 1992). In summary, gross nitrification rates, microbial NO_3^- assimilation, and microbial N retention in forests may be greater and more widespread than previously thought.

Sequestration of N in woody residues.—Sequestration of ^{15}N in woody residues and debris in soil was reported for a coniferous forest in California (Schimel and Firestone 1989). Nitrogen flow from soil to decomposing litter (presumably via fungal translocation) may also be an important mechanism of N retention (Hart et al. 1993). Many litter decomposition studies have found that the N content of litter increases in the early stages of decay (Swift et al. 1979). Recalcitrant conifer litter and coarse woody debris are generally considered to be sites of N immobilization because of high C:N ratios (about 500:1; Van Miegroet et al. 1990). During the first 7 yr of decomposition, however, leaching was a pathway of N loss from logs, and N and other nutrients were also exported from logs via fungal sporocarps, from which NO_3^- can be leached (Harmon 1992, Harmon et al. 1994). Although N losses from logs were small, these results suggest that past models of the N dynamics of woody detritus may need revision. Logs are also known to be sites of N_2 fixation (Harmon et al. 1986, Harmon 1992), which may also increase the N source strength of logs.

Abiotic retention.—Little is known of the mechanisms and importance of abiotic N retention in soils. Conceptual models of soil N cycling in the ecological literature show all organic N first passing through microbes, without considering potentially important nonbiological processes (Johnson 1992). A re-examination of soil N cycling processes in natural systems is needed, which should include the information supplied in the agricultural literature over the last 50 yr. A substantial proportion (10–50%) of soil organic N is typically in humin (i.e., soil organic matter that is not digested in a solution of HCl (6 mol/L) (Cheng and Kurtz 1963, Keeney and Bremner 1966, Jorgensen 1967, Johnson 1979, Stevenson 1982), and some studies indicate that the mechanisms of N incorporation into humus are partially nonbiological in nature. The inhibitory effect of lignin on decomposition and N mineralization (Cromack 1973, Melillo et al. 1982, Berg et al. 1984, Berg and McClaugherty 1987) is due in part to the formation of stable nitrogenous compounds from lignin by-products, reducing N availability to decomposer organisms (Berg et al. 1984). Physical condensation reactions of

TABLE 3. Nitrogen budgets, soil base saturation, and soil solution concentrations in coniferous forests at the Findley Lake, Washington; Whiteface, New York; and Smokies, North Carolina sites (Johnson and Lindberg 1992).

Parameter	Findley Lake	Whiteface	Smokies
N deposition ($kg \cdot ha^{-1} \cdot yr^{-1}$)	2.0	15.9	27.1
Biomass N increment ($kg \cdot ha^{-1} \cdot yr^{-1}$)	3.6	10.8	1.8
Nitrogen leaching ($kg \cdot ha^{-1} \cdot yr^{-1}$)	0.1	3.0	20.7
Soil C:N ratio	33	20	9
Base saturation, A horizon (%)†	13	11	4
Base saturation, B horizon (%)†	4	7	4
Soil solution NO_3^- ($\mu mol_c/L$)‡	<1	26	94
Soil solution SO_4^{2-} ($\mu mol_c/L$)‡	31	163	131
Soil solution pH‡	5.7	4.7	4.3
Soil solution Al^{3+} ($\mu mol_c/L$)‡	8	39	56

Notes: The Findley Lake site (1130 m) is located 65 km southeast of Seattle and is dominated by ~180-yr-old Pacific silver fir (*Abies amabilis*). The Whiteface Mountain site (summit elevation 1483 m) is located near Wilmington, New York, in the northeast section of the Adirondack Mountains. Data were collected between 970 and 1100 m elevation. Balsam fir (*Abies balsamea* [L.] Mill.), red spruce (*Picea rubens* Sarg.), and white birch (*Betula papyrifera* var. *cordifolia* [Reg.]) dominated the study area. The Smokies site (1740 m) is located in the Great Smoky Mountains National Park in western North Carolina and was mainly old-growth (200–300-yr-old) red spruce with a minor yellow birch (*Betula alleghaniensis* Britt.) component.

† Ammonium chloride cation extraction method. Base saturation data are from D. Johnson (*personal communication*).

‡ Soil solution concentrations are weighted average values.

phenols (originating from partially degraded lignin and some fungal pigments) with either amino acids or ammonia result in the formation of "brown, nitrogenous humates" (Mortland and Wolcott 1965, Nommik 1965, Nommik and Vahtras 1982, Paul and Clark 1989). These nonbiological, autocatalytic reactions are important in the production of humus (Mortland and Wolcott 1965, Paul and Clark 1989).

Nitrogen outputs

The primary pathways of N loss from forest ecosystems are hydrological transport of organic and inorganic N (mainly as NO_3^-) beyond the rooting zone into groundwater or streamwater, N loss in surface flows, and N loss associated with soil erosion losses. Gaseous N compounds are also produced via nitrification and denitrification, which are emitted to the atmosphere or dissolved in water and hydrologically transported until degassed to the atmosphere (Bowden and Bormann 1986, Davidson and Swank 1990). Periodic pulses of N are lost from the forest during fires, which volatilize N (Raison et al. 1985). Fire-released N in the soil may be nitrified, much of which may be leached or exported from the forest by surface waters (Dunn et al. 1979, Riggan et al. 1994). Ammonia gas can be emitted from alkaline soils or from N-rich plants (Langford and Fehsenfeld 1992, Sutton et al. 1993) and lost from the system. Harvesting activities remove large quantities of N and other nutrients from the ecosystem and may prevent N saturation, even with high N deposition.

Comparison of N inputs, retention, and outputs in spruce–fir ecosystems

The apparent relationship between N inputs, biological N retention, and N outputs can be illustrated by comparing three high-elevation coniferous forest sites included within the Integrated Forest Study (IFS) of 16 forests located mainly in North America (Johnson and Lindberg 1992; Table 3). The Findley Lake site in the Cascade Mountains of Washington state is a relatively unpolluted site, receiving N and S inputs an order of magnitude lower than those at spruce stands in the Great Smoky Mountains, North Carolina and in the Whiteface Mountains, New York. At Findley Lake, the biological demand for N is high relative to deposition, as indicated by the fact that the increment of N in aggrading biomass is greater than N deposition. The soil C:N ratio is relatively high, and N leaching is minimal (Table 3). The soil C:N ratio is lower at Whiteface than at Findley Lake, indicating a lesser biological demand for N by soil organisms, but biomass increment is higher, and thus leaching is only moderately greater than at Findley Lake. At the Smokies site, N deposition is greatest and the soil C:N ratio and biomass increment are very low; thus, NO_3^- leaching is high.

CHARACTERISTICS PREDISPOSING FORESTS TO NITROGEN SATURATION

Nitrogen-saturated forests in North America exhibit wide variability in the degree of N loss relative to atmospheric N inputs. In the IFS, no strong correlation was found across all sites between estimated atmospheric N input and measured NO_3^- leaching below the rooting zone (Van Miegroet et al. 1992*b*). However, if only those sites currently leaching NO_3^- are considered, the relationship between input and output fluxes is stronger. Obviously N deposition alone does not control N saturation (Dise and Wright 1995, Näsholm et al. 1997), although N deposition may accelerate and exacerbate the development of N saturation. In many re-

gional studies the degree of N saturation and the level of N deposition inputs are closely related (Johnson and Lindberg 1992, Stoddard 1994, Jeffries 1995, Bytnerowicz and Fenn 1996, Williams et al. 1996*a*). Much of the variability in ecosystem N loss seems to be explained by differences in stand age and successional status (Vitousek and Reiners 1975, Peet 1992), species composition (Van Miegroet and Cole 1984, Aber et al. 1995), climate, soil N pool size (Cole et al. 1992, Van Miegroet et al. 1992*a*, Stoddard 1994), past management, and land use (Feger 1992, Magill et al. 1996). Forests prone to developing symptoms of N saturation typically have low net primary productivity (NPP), high N deposition, and high soil N reserves; they are limited by other factors (e.g., P, short growing season); and they are in the late successional stages. Even forests with elevated N loss commonly continue to accumulate N, apparently in soil and the forest floor. When a major disturbance such as an insect infestation, harvesting, or fire occurs, a period of especially high N losses from the ecosystem can be expected (Riggan et al. 1994).

Stand vigor, successional stage, and forest type

Aggrading forests with high nutrient demand that are still accumulating N are less likely to become N saturated. Nitrogen-saturated forests are often characterized by trees that are not highly conservative of N and that exhibit high N turnover in the canopy (Johnson and Lindberg 1992). Older, stagnated stands, such as the high-elevation spruce site in the Great Smoky Mountains and the mixed hardwood forest at Turkey Lakes in Ontario, Canada, are N saturated, with high levels of NO_3^- leaching (Van Miegroet et al. 1992*b*). These sites are characterized by moderate to high N deposition, large N stores in soil, low soil C:N ratios, high nitrification rates, and moderate to low N uptake by trees.

Streamwater NO_3^- concentrations have been related to forest successional stage in the eastern United States (Likens et al. 1970, Vitousek and Reiners 1975). Nitrate concentrations were high after disturbances such as clearcutting and in mature ecosystems, but lower in mid-successional forests. Peet (1992) reviewed a model of four stages of forest development and nutrient retention strength. In the establishment phase, biotic demand is low and the system is "leaky." In the thinning stage, nutrients are sequestered in accumulating biomass and nutrient losses are low. In the transition phase, mortality increases and nutrient losses slowly increase as biotic accumulation decreases. As the forest approaches steady state with relatively constant biomass, nutrient losses balance nutrient influx.

Nutrient retention in some eastern and western forests in North America may operate on different time scales (Blew and Edmonds 1996). A 600-yr-old forest in Washington was still increasing in basal area, and plant retention of N was more important than generally thought for mature forests (Edmonds et al. 1995). Thus, nutrient retention in old-growth forests in the Pacific Northwest may function more like mid-successional forests in the eastern United States (Blew and Edmonds 1996).

Hedin et al. (1995) compared patterns of nutrient loss from 31 small old-growth watersheds in a remote area in southern Chile to old-growth forests in North America with varying levels of N deposition inputs. Results generally supported the "nutrient-retention hypothesis" (Vitousek and Reiners 1975, Gorham et al. 1979), which states that unpolluted old-growth forests exhibit minimal or no net biotic nutrient retention (Hedin et al. 1995). In the pristine forests, 95% of hydrologic N losses were as dissolved organic N and inorganic losses were minimal (4.8% of total N as NH_4^+ and 0.2% as NO_3^-). The 31 old-growth pristine watersheds can be classified alternatively as "non-leaky" or "leaky" depending on whether inorganic or organic N forms are considered. Significant NO_3^- export only occurred in old-growth forests with anthropogenic N inputs. Nitrate : ammonium ratios in streamwater were generally ≤ 1 in pristine old-growth forests, but were consistently above 8 in waters draining old-growth forests with high N deposition in the eastern United States (Hedin et al. 1995). Hedin et al. (1995) hypothesized that old-growth forests are particularly sensitive indicators of ecological effects of N deposition, since these ecosystems are inherently poor at retaining added nutrients.

Effects of forest type on susceptibility to N saturation is illustrated with alder-dominated stands in the Pacific Northwest. Alder growing on gravelly granitic soil at Cedar Creek, Washington, had large losses of NO_3^- because of high N_2 fixation rates (Van Miegroet and Cole 1984). However, alder stands growing on weatherable sandstone soils at Cascade Head, Oregon, accumulated 20 Mg N/ha with little NO_3^- loss (Franklin et al. 1968, Bormann et al. 1993*b*). The experimental work in the Harvard Forest, Massachusetts, also demonstrates differences in N retention between forest types. Nitrogen saturation was induced by N addition in conifer stands, while the hardwood stands retained and accumulated N in soil with little N leaching (Aber et al. 1995).

Previous land use or stand history

Land-use history is a major factor determining the N retention capability of a forest stand (Feger 1992). In the Harvard Forest, previously tilled sites exhibited net nitrification, but continually wooded sites and previously pastured sites did not. Magill et al. (1996) concluded that differences in previous land-use history in northeastern forests had a greater effect on current N cycling rates than differences in cumulative N deposition. Logging history is a major variable affecting watershed export of NO_3^-. In the Great Smoky Mountains National Park on the Tennessee–North Carolina border, NO_3^- concentrations were significantly lower in

streams of watersheds that had been logged prior to the park's establishment in 1936 than in unlogged watersheds at similar elevations (Silsbee and Larson 1982). The authors concluded that second-growth forest in the logged areas was more effective in retaining N due to greater nutrient demand in the aggrading forest compared to unlogged mature forest stands.

Fire history can have major effects on ecosystem N balance (Hornbeck et al. 1997). Low- to moderate-intensity fires generally enhance N retention in the long term by reducing site N capital and increasing postfire vegetative demand (Dow and DeWalle 1997). High-intensity fires adversely affect soil structure, organic matter content, nutrient status, and plant productivity. The ecological effects of fire vary greatly depending on fire characteristics, climate, soil, and plant species adaptations to fire (Kimmins 1997). We can only generalize that forests that aggrade after fire should have high N retention capacity.

Soil N accumulation

In the IFS (Johnson and Lindberg 1992) soils with a C:N ratio >20 were more effective in retaining N than soils with a C:N ratio ≤10 (Table 3). Net N mineralization rates and NO_3^- leaching were greatest in soils with high total N content (>5000 kg/ha) between 0 and 60 cm soil depth and an overall C:N ratio <20 (Cole et al. 1992). Several studies have reported high N accumulation in soil and low C:N ratios in N-saturated forests (McNulty et al. 1991, Aber 1992, Nohrstedt et al. 1996).

Topography and climate

Physical factors such as slope steepness and climate strongly affect ecosystem N retention. In central Ontario, steeper watersheds lost more N than those with gentler grades (Dillon and Molot 1990). In cold, snowmelt-dominated systems, much of the total annual N flux can occur during early snowmelt periods (Campbell et al. 1995*a*, Baron and Campbell 1997). Short growing seasons inhibit forest N uptake ability. In the Colorado Front Range, physical constraints on N uptake, including slope steepness, rapid snowmelt, and short growing seasons combine to enhance watershed N loss (Campbell et al. 1995*a*, Baron and Campbell 1997).

Ecosystem Responses to Excess N

Nitrate leaching and export

Excessive loss of NO_3^- is the cardinal sign of an N-saturated ecosystem. However, forests that are stagnant, in decline, or have been disturbed (Swank 1988) may export high NO_3^- levels because of decreased plant demand for N or because of other disturbance effects on nutrient cycling. Such forests may be considered N saturated based on high leachate loss of NO_3^- and other symptoms, although N saturation may only be a result of the decline and not a causal factor.

Climatic effects.—Climate plays a major role in influencing NO_3^- fluxes through the soil profile and within the watershed because hydrologic flows, NO_3^- transport, nitrification rates, and biological uptake are all influenced by temperature and precipitation. Seasonal precipitation patterns exert a major influence on NO_3^- losses from ecosystems, especially when major hydrologic flows in soil from precipitation or snowmelt leach significant quantities of NO_3^- from the main rooting zone during the off-season before significant plant N uptake begins (Riggan et al. 1985).

The effect of climate extremes and trends on NO_3^- release and export was elegantly demonstrated from four watersheds in the northeastern United States: East Bear Brook, Maine; Watershed 6, Hubbard Brook, New Hampshire; Arbutus Watershed, Huntington Forest, Adirondack Mountains, New York; and Biscuit Brook, Catskill Mountains, New York (Mitchell et al. 1996*a*). Nitrate loss patterns from these watersheds were highly synchronous from 1983 through 1993. In the months after an unusually cold period in December 1989, when soil freezing was much more severe than usual, NO_3^- losses in streamwater and in soil solution were notably higher. In subsequent years, NO_3^- concentrations and fluxes decreased at all sites. The authors suggested that the severe freeze in December 1989 and NO_3^- transport during the remainder of the dormant season may have hastened the release of labile N and contributed to decreases in NO_3^- losses in recent years (Mitchell et al. 1996*a*).

Global warming may exacerbate N saturation by stimulating net N mineralization and nitrification rates, leading to greater availability of soil N (Ulrich 1983, Van Miegroet and Johnson 1993). If warming also increases NPP, then N retention and storage in plant biomass will also be greater. In areas with soil moisture deficits, temperature-induced increases in NO_3^- losses are likely to be smaller. Increased NO_3^- release in soil with increased soil temperatures, presumably from increased rates of N mineralization and nitrification, have been reported in the red spruce forest at Whitetop Mountain in southwestern Virginia (Joslin and Wolfe 1992, 1993). Increased drainage losses of NO_3^- in the Adirondacks and Catskills in New York and from Hubbard Brook in New Hampshire during 1989–1991 may be related to the warmer and wetter conditions prevailing during this period (Mitchell et al. 1996*b*) and/or to the severe soil freezing in December 1989 (Mitchell et al. 1996*a*).

Soil porosity and hydrologic fluxes.—Even N-limited ecosystems can lose high levels of NO_3^- if soils are highly porous. Annual N retention was low (40–62%) in an aggrading N-limited forest growing on sandy soil in a coastal watershed in Waquoit Bay, Massachusetts (Lajtha et al. 1995). Nitrogen was effectively retained during the summer, except in months with very high rainfall events. During the dormant season, NO_3^- was released in proportion to water flux through the

forest floor. Many studies have found export of NO_3^- or of other ions to increase with increasing stream flow (Riggan et al. 1985, Kelly 1988, Jaworski et al. 1992, Murdoch and Stoddard 1992, Hill 1993, Campbell et al. 1995*b*). Temporal patterns of hydrologic fluxes interact with biotic uptake and internal cycling patterns in determining ecosystem N retention. Leaching of NH_4^+ may be greater in systems with chronic inputs of sea salt spray, because of cation exchange reactions in soil (Duckworth and Cresser 1991, Lajtha et al. 1995).

N leaching in response to N additions.—Nitrogen additions (total annual N loading of 33.6 $kg \cdot ha^{-1} \cdot yr^{-1}$) to a 40–60-yr-old mixed northern hardwood forest catchment (Bear Brook, Maine) resulted in elevated NO_3^- fluxes and concentrations in streamwater, especially in the second and third years after the treatments began (Kahl et al. 1993). Nitrate concentrations were as high as 90 $\mu mol_c/L$ during episodes (Norton et al. 1994). Seasonal patterns of streamwater NO_3^- concentrations were altered by the N treatment, with NO_3^- loss from the treated catchment occurring nearly year-round. Symptoms of N saturation were induced at lower rates of N deposition than previously believed, and the rapid increase in streamwater NO_3^- concentrations was surprising. Watershed retention of N inputs (deposition plus fertilization) from mass balance estimates were 73–86% in the three treatment years. Norton et al. (1994) concluded that watershed responses were dominated by chemical changes in shallow soils. The relatively low retention of N at Bear Brook, high foliar N, low soil C:N, and high rates of net N mineralization indicated that, prior to treatment, the forest was in the incipient stages of N saturation, although N export in streamwater was relatively low (2.8 $kg \cdot ha^{-1} \cdot yr^{-1}$).

Estimated annual wet plus dry N deposition at Bear Brook is 4.6 $kg \cdot ha^{-1} \cdot yr^{-1}$ (Magill et al. 1996), suggesting that in some forests with relatively low N deposition, net N retention may rapidly decline with increasing N inputs. Recovery in these systems is also rapid following decreased N inputs. In plot-level studies at Bear Brook, N and S amendments were given for 4 yr and caused dramatic increases in soil solution NO_3^-. However, NO_3^- concentrations in soil solution returned to pretreatment levels within several months following termination of the N treatments. Rustad et al. (1996) concluded that the soils had little or no capacity for NO_3^- sorption, and that any NO_3^- adsorbed would be quickly immobilized by biological uptake and transformed to organic forms.

Case studies in North America.—The Fernow site in West Virginia (mixed hardwood forest) is probably the best example in North America where the progressive development of N saturation in a forest ecosystem is documented with long-term data (Edwards and Helvey 1991, Adams et al. 1994, 1997, Peterjohn et al. 1996). Nitrate export and streamwater NO_3^- concentrations have increased steadily over the past two decades, and NO_3^- concentrations now exhibit little seasonal variability (monthly averages ranged from 44 to 64 $\mu mol_c/L$ from 1984 to 1994; Peterjohn et al. 1996), demonstrating the severity of N saturation in this ecosystem. High NO_3^- discharge also occurred from a young aggrading forest, and NO_3^- export increased rapidly after fertilization (Peterjohn et al. 1996). Some undisturbed watersheds in southwestern Pennsylvania also show increasing NO_3^- concentrations in streamwater in recent years (46 $\mu mol_c/L$ median concentration for November 1991–February 1995) (Dow and DeWalle 1997).

High NO_3^- concentrations (ranging from 50 to 100 $\mu mol_c/L$) occur in streams draining undisturbed watersheds in the Great Smoky Mountains in Tennessee and North Carolina. Nitrate concentrations were highest at higher elevations and in areas of old-growth spruce–fir forest that have never been logged (Stoddard 1994, Flum and Nodvin 1995). Nitrogen concentrations in streams were frequently greater than concentrations in deposition. Similarly, at the Smokies site in the IFS (Johnson et al. 1991), N loss from the forest stand (20 $kg \cdot ha^{-1} \cdot yr^{-1}$) was nearly equal to N deposition (27 $kg \cdot ha^{-1} \cdot yr^{-1}$).

In the western United States, the most dramatic case linking N deposition and elevated watershed N export is in the Los Angeles Air Basin, where dry deposition of N is possibly the highest in North America (Bytnerowicz and Fenn 1996). Streamwater NO_3^- fluxes from polluted chaparral watersheds in the San Gabriel Mountains near Los Angeles were one to three orders of magnitude greater than in unpolluted watersheds (Riggan et al. 1985). Nitrogen deposition was estimated to be 2.3 times higher than the N accretion rate of the N_2-fixing *Ceanothus* stands. Discharge rates in two chaparral and two grassland watersheds over 4 yr ranged from 0.04 to 19.4 kg $N \cdot ha^{-1} \cdot yr^{-1}$. Sharp NO_3^- concentration peaks occurred during the first winter storms, when the ecosystem was loaded with N accumulated during the dry summer months. Streamwater NO_3^- concentrations averaged 193 $\mu mol_c/L$ in 35 streams from chaparral watersheds in the San Gabriel Mountains after a major storm in March 1982. Wildfire mobilized N that had accumulated in the chaparral ecosystems from chronic N deposition. Nitrate concentrations as high as 1120 $\mu mol_c/L$ were found in streamwater from severely burned watersheds exposed to high levels of N deposition (Riggan et al. 1994). In contrast, burned chaparral watersheds in the Los Angeles Basin and in Arizona with relatively low N deposition did not exhibit high NO_3^- levels in streamflow. We have routinely measured NO_3^- concentrations >100 $\mu mol_c/L$ with a peak value of 350 $\mu mol_c/L$ in undisturbed small watersheds receiving high atmospheric N deposition in the San Bernardino Mountains east of Los Angeles (M. E. Fenn and M. A. Poth, *unpublished data*).

High NO_3^- concentrations in surface waters of high-elevation tundra and spruce–fir forest watersheds in the

Colorado Front Range are coincident with high N deposition from regional agricultural and urban sources. Watersheds in Colorado that receive lower N deposition have low N concentrations in their waters (Stottlemyer and Troendle 1995, Williams et al. 1996*a*).

Eutrophication of estuaries and coastal marine ecosystems

Nitrogen loss from terrestrial watersheds can constitute a significant N source for estuaries (Hinga et al. 1991, Paerl 1995, Jaworski et al. 1997). The combination of N deposition to the sea and to coastal watersheds with upland land-use changes has resulted in large nutrient inputs to coastal waters. Estuaries are now among the most intensely fertilized ecosystems on earth, receiving far more nutrient inputs than other systems (Howarth 1988, Lajtha et al. 1995, Howarth et al. 1996). Eutrophication of estuaries and coastal marine ecosystems is a growing problem, and N inputs need to be reduced to prevent or reverse eutrophication (Nixon 1990, 1995). Nutrient loads in coastal waters of the eastern U.S. seaboard (Jaworski et al. 1997) and the northern coast of Europe have led to higher frequency of algal blooms, increased severity of low-oxygen conditions, and episodic death and long-term decline of marine organisms (Fisher and Oppenheimer 1991). Nitrogen inputs and the N:P ratio of inflows to estuaries are particularly critical because many northern temperate marine ecosystems are N limited, in contrast to most freshwater systems that are P limited (Howarth 1988). However, some estuaries may be P limited or switch seasonally between P and N limitation.

The Chesapeake Bay is a prime example of anthropogenic nutrient inputs that contribute to eutrophication of coastal waters (Jaworski et al. 1997). Atmospheric N deposition, sewage, and agriculture each reportedly account for approximately one-third of the anthropogenic N loading to the bay (Fisher and Oppenheimer 1991, Hinga et al. 1991). Eutrophication in Chesapeake Bay is resulting in an increasingly large volume of anoxic bottom waters (Officer et al. 1984), and may be the cause for the loss of striped bass from the bay (Price et al. 1985). Nitrogen deposition was also calculated to contribute from 10 to over 50% of the anthropogenic loading in six other coastal marine ecosystems in eastern North America (Fisher and Oppenheimer 1991, Hinga et al. 1991, Paerl 1995).

Toxicity of surface waters

Elevated concentrations of NO_3^-, reduced acid-neutralizing capacity, and increased acidity and Al^{3+} concentrations in streamwater of N-saturated watersheds can exceed the tolerance threshold of sensitive aquatic organisms. Field and laboratory evidence suggests that acute and chronic toxic impacts are possible as a consequence of N-induced changes in surface water chemistry (Kincheloe et al. 1979, Zischke et al. 1983, Magnuson et al. 1984, Lemly and Smith 1987, Ingersoll et al. 1990*a*, *b*). Episodic acidification was studied in 13 small streams in the Adirondack region of New York, in the Catskills of New York, and in the northern Appalachian Plateau, Pennsylvania (Baker et al. 1996). Streams with moderate-to-severe episodic acidification during high flow had higher fish mortality and lower brook trout density and biomass compared to nonacidic streams. Brook trout moved downstream during episodic events. Trout abundance was reduced and acid-sensitive fish were absent from streams with median pH <5.0–5.2 and inorganic Al^{3+} >3.7–7.4 $\mu mol_c/L$ during high flow. Nitrate concentrations were low in the Pennsylvania streams, but the Catskill and Adirondack streams had high NO_3^- concentrations and large episodic pulses (≤ 54 $\mu mol_c/L$). High baseline concentrations of SO_4^{2-} occurred in all three study areas, and high baseline NO_3^- concentrations were measured in the Adirondacks and Catskills (Wigington et al. 1996). Baker et al. (1996) concluded that atmospheric deposition contributed to the severity of episodes in the streams, and that episodic acidification can have long-term effects on fish communities in small streams.

Nitrogen mineralization and nitrification

Nitrogen availability is largely determined by net N mineralization rates, which are usually far greater that N deposition fluxes. Nitrogen mineralization rates are generally higher in deciduous forests than coniferous forests (Vitousek and Melillo 1979, Nadelhoffer et al. 1985). Warm temperatures and soil properties that enhance soil moisture-holding capacity are associated with higher net N mineralization rates. Nitrogen mineralization and nitrification are also greater in forest soils containing large amounts of labile organic matter with low C:N ratios (Nadelhoffer et al. 1983, McNulty et al. 1991, Attiwill and Adams 1993, McNulty et al. 1996). In the Integrated Forest Study (IFS), N mineralization was the factor most highly correlated with NO_3^- leaching. Net N mineralization and N deposition accounted for 64% of the variability in N losses among the 16 IFS sites (Van Miegroet et al. 1992*a*), emphasizing the importance of internal and external N sources in contributing to N excess.

As stands age and accumulate organic N in soil and in the forest floor, and as plant N demand diminishes, net N mineralization and nitrification can produce large amounts of NO_3^-, which may leach from the system if biotic N demand is insufficient to retain the available N. Atmospheric N deposition can contribute to sustained leaching losses from the system. This scenario seems to be largely responsible for the high NO_3^- leaching rates in the overmature forest at the Smokies Tower site in the Great Smoky Mountains in North Carolina (Johnson et al. 1991, Johnson and Lindberg 1992). Nitrate from N mineralization in the Turkey Lakes Watershed in Ontario, Canada (Foster et al. 1989*a*) accounted for nearly all of the NO_3^- leached from the forest (17.9 to 23.6 kg $N \cdot ha^{-1} \cdot yr^{-1}$).

Inorganic N added to soils has frequently been shown to initially stimulate N mineralization (McNulty et al. 1990), an effect known as the priming effect or "added nitrogen interaction" (Haynes 1986, Rao et al. 1991). The nature of the positive priming effect of added N is controversial. The most general explanation of the priming effect is a result of temporary immobilization of the added N, followed by re-mineralization (Haynes 1986). It has also been suggested that chronic N inputs increase nitrification rates by maintaining greater populations of nitrifier organisms in soil (Johnson 1992, Van Miegroet and Johnson 1993). If this is true, N deposition indirectly increases NO_3^- leaching by stimulating nitrification. In the long term, N mineralization may decline as N accumulates in soil (Aber et al. 1995).

Effects on soil organic matter

Nitrogen deposition is expected to alleviate N deficiency and increase C sequestration in the biomass and soil organic matter of temperate forests (Galloway et al. 1994, Nilsson 1995). Litter accumulation in the forest floor is enhanced in an N-rich environment due to increased litter production (Bray and Gorham 1964, Majdi and Bergholm 1995) and decreased long-term decomposition rates. The early phases of litter decomposition have been reported in many cases to be stimulated by higher N concentrations in litter, although others have reported a negative effect or no relationship between litter N concentration and decomposition rate (Prescott 1995). However, later stages of litter decomposition are retarded with higher N concentrations (Berg et al. 1987, 1995, Fog 1988, Melillo et al. 1989, Nilsson 1995). Decreased decomposition of N-rich litter may be due to the formation of stable nitrogenous compounds from lignin by-products (Berg et al. 1995). Organic matter accumulation has frequently been observed in forests with chronic N inputs from fertilization, N deposition, or N_2 fixation (Bormann et al. 1993*b*, Kuyper 1994, Fenn et al. 1996, Martikainen 1996). The potential for added N to increase ecosystem C storage has been demonstrated in grasslands, forests, and tundra (Billings et al. 1984, Hunt et al. 1988, Rastetter et al. 1991, Nilsson 1995). However, Wedin and Tilman (1996) found that long-term N additions in Minnesota grasslands dominated by C_4 prairie grasses led to increased NO_3^- loss and low soil C sequestration rates as a result of N-induced shifts to C_3 nonnative grasses that have lower C:N ratios. Others have argued that increased atmospheric CO_2 levels are likely to increase the C:N ratio and C storage of the C_3 plants, thus at least partially counteracting the processes that limited C storage in the N-rich plots (Hungate et al. 1997).

Soil acidification, base cation depletion, Al toxicity, and plant nutrition

In several studies in the northeastern United States, forests exposed to elevated N and S deposition have experienced marked declines in total Ca and Mg (Federer et al. 1989, Miller et al. 1993, Lawrence et al. 1995, Likens et al. 1996). Nutrient-cation depletion may be caused by a number of factors including the leachate loss of cations as counterbalancing ions for leached SO_4^{2-} and NO_3^-, reduced cation exchange sites resulting from higher Al^{3+} availability and lower pH, and decreased atmospheric deposition of cations in recent years (Matzner and Murach 1995, Likens et al. 1996). Deposition of N and other acidic pollutants can further acidify soils that are inherently acidic and low in cations, and increase the risk of Al toxicity or nutrient cation deficiency (Johnson et al. 1991). This is perhaps best illustrated in red spruce forests in the Great Smoky Mountains of North Carolina, where forest characteristics and symptoms of excess N deposition are highly similar to cation-deficient systems described for central Europe (Schulze 1989). These systems are N-saturated and exhibit borderline deficiencies of Ca and/or Mg (Johnson et al. 1991, Van Miegroet and Johnson 1993).

Although SO_4^{2-} and NO_3^- are of nearly equal concentrations in soil solution on average at the Smokies site, the peak concentrations of cations and anions are driven primarily by peak concentrations in NO_3^-. During these NO_3^- pulsing episodes, Al^{3+} and the Al:Ca ratio in soil solutions increase considerably above baseline levels, and at times exceed threshold values found to cause reduced base cation uptake in laboratory studies (Raynal et al. 1990). Fertilization studies with combinations of Ca and Mg indicated incipient cation deficiency at an upper elevation site, but not at a less acidic lower elevation site (Van Miegroet et al. 1992*a*).

High rates of N and S deposition are not necessary to create acidic soil conditions. Extremely acidic soils, mostly Spodosols, occur in pristine as well as polluted forest ecosystems. The soils at Findley Lake, Washington, are extremely acidic, despite the low deposition rates, with base saturation values in the range of the more polluted Smoky Mountains and Whiteface, New York, sites. Although the differences in deposition are not reflected in soil acidity, they are clearly reflected in soil solution acidity. Because of the greater deposition of N and S at the Whiteface and Smokies sites, the concentrations of SO_4^{2-} and NO_3^- in soil solution are much greater than at Findley Lake, resulting in greater Al^{3+} concentrations and lower pH (Table 3).

Foliar nutrient responses

Increased foliar N and N:nutrient ratios are nearly universal phenomena in N-saturated forests, and N:cation and N:P (Koerselman and Meuleman 1996, Verhoeven et al. 1996) ratios are commonly used as measures of N enrichment. Nutrient imbalances in trees expressed as root or foliar element ratios, (e.g., Ca:Al and Mg:N) have been linked to reductions in net photosynthesis, photosynthetic N use efficiency, forest growth, and tree mortality (Friedland et al. 1988, Shortle and Smith 1988, Schulze 1989, Richter et al. 1992,

McNulty and Aber 1993, Cronan and Grigal 1995, Likens et al. 1996, McNulty et al. 1996). Higher N:P ratios have been reported in areas of higher N deposition in big cone Douglas-fir (Zinke 1980) and ponderosa pine (Fenn et al. 1996) in southern California, along an elevational and deposition gradient in bristlecone pine in the Colorado Front Range (Williams et al. 1996*a*), in Norway spruce (*Picea abies* [L.] Karst.) in Sweden (Ericsson et al. 1993), and in Douglas-fir in The Netherlands (Mohren et al. 1986).

Amino acids, especially arginine, accumulate in the foliage of plants growing in areas with high N deposition (Van Dijk and Roelofs 1988, Edfast et al. 1990, Ericsson et al. 1993, Nohrstedt et al. 1996, Näsholm et al. 1997). In Norway spruce, N:P ratios were correlated with free arginine concentrations in foliage (Ericsson et al. 1993). Nitrogen can also be stored in foliage as NO_3^-, but not until N growth requirements are satisfied (Zhen and Leigh 1990), or the capacity for NO_3^- assimilation is exceeded (Lee et al. 1986). Bracken fern (*Pteridium aquilinum* var. *pubescens* Underw.) and overstory species at a high-deposition site in the San Bernardino Mountains in southern California accumulated significantly higher concentrations of NO_3^- than the same species at a low-deposition site (Fenn et al. 1996). Similar findings were also reported for an oak–birch forest in The Netherlands (Stams and Schipholt 1990). Bracken fern has been shown to accumulate high concentrations of total N (Gerloff et al. 1966) and to accumulate NO_3^- to a greater degree than the other species sampled in California and in The Netherlands.

Greenhouse gas fluxes

Nitrogen saturation of terrestrial ecosystems may dramatically alter fluxes to the atmosphere of radiatively active gases (e.g., CO_2, NO, N_2O, CH_4). Net C balance is expected to respond to chronic N inputs differently as the forest progresses through more advanced stages of N saturation. The net effect of N on C sequestration will depend on the relative effects of altered N status on C fixation in plant biomass vs. effects on decomposition of litter and soil organic matter (Shaver et al. 1992).

Nitrogen availability influences fluxes of nitric oxide (NO), nitrous oxide (N_2O) and methane (CH_4) (Castro et al. 1994, Nilsson 1995, Sitaula et al. 1995*b*). Higher N levels in soil generally result in higher emissions of N trace gases (Matson and Vitousek 1990, Bronson and Mosier 1993, Castro et al. 1994, Sitaula et al. 1995*a*, Fenn et al. 1996). In forests in eastern North America, N_2O seems to be the dominant N trace gas produced in soil, while in California, where soils are often coarse textured and well drained, NO emissions are much greater than N_2O emissions (Anderson et al. 1988, Davidson 1993, Fenn et al. 1996). Nitrification seems to be the dominant process for production of NO in soils of western forests (Anderson et al. 1988, Davidson 1992, 1993), whereas N_2O is generally produced by denitrification (Davidson 1992).

Castro et al. (1995) reported that CH_4 consumption by forest soils was greatest in more fertile sites at the Harvard Forest, Massachusetts, but in N-fertilized soils CH_4 consumption rates were 15–64% lower than in unfertilized stands. Methane consumption in soil is reduced by N additions to soil, possibly as a result of interference by NH_4^+ at the site of CH_4 oxidation (Steudler et al. 1989, Mosier et al. 1991, Williams and Fehsenfeld 1991, Sitaula et al. 1995*a*).

Anomalous cases of ecosystem responses

Anomalous cases of unexplainably high N retention with little loss (Aber et al. 1995), or high export of N with little outside input or N_2 fixation (Foster et al. 1989*a*, *b*), may provide opportunities to test hypotheses of processes critical to N retention in forests.

Turkey Lakes, Ontario, Canada.—In the Turkey Lakes Watershed in south central Ontario, Canada, throughfall N inputs (7.7 $kg \cdot ha^{-1} \cdot yr^{-1}$) were low to moderate compared to more urban regions, yet NO_3^- leaching from this old-growth forest was 2.4 times throughfall N inputs. Approximately 25% of the leached NO_3^- was from atmospheric deposition and 75% from mineralization and nitrification of organic soil N stores (Foster et al. 1989*a*). Nitrogen deposition may accelerate the rate at which these forests reach N saturation. Streamwater NO_3^- concentrations at Turkey Lakes in 1984 ranged from ~35 to 105 $\mu mol_c/L$ (Foster et al. 1989*b*), and losses were clearly related to catchment grade and water discharge (Dillon and Molot 1990). Nitrogen losses from mineralization and nitrification cannot exceed N inputs indefinitely. This may present opportunities to test how future watershed N losses will depend on the balance between vegetative and microbial N demand, abiotic N retention, N deposition, N mineralization and nitrification rates, and possibly N_2 fixation.

Pacific Northwest.—Oregon, Washington, and Alaska have lower N inputs in bulk precipitation (0.5–2.0 $kg \cdot ha^{-1} \cdot yr^{-1}$) than most other regions of North America (Tiedemann et al. 1988, Weathers et al. 1988, NAPAP 1993). However, cloudwater deposition can double N inputs in some fog-dominated coastal and mountain forests (Harr 1982, Bormann et al. 1989) and elevated N concentrations in bulk precipitation and cloudwater have been measured downwind of urban centers. Low atmospheric N inputs, a long growing season, cation-rich soils, and N deficiency suggest that problems with N saturation should be minimal in the Pacific Northwest. Symptoms of N saturation, however, have been observed in some forests in the Pacific Northwest and Alaska, including negative or no response to N fertilizer, declining pH and cation availability in developing Spodosols, and localized NO_3^- and cation losses. Hypotheses to explain negative responses to fertilization of stands of Douglas-fir (*Pseudotsuga menziesii* [Mirb.]

Franco) and western hemlock (*Tsuga heterophyla* [Raf.] Sarg.) (Miller et al. 1986) include large N capital and P limitation in Douglas-fir soils (Radwan et al. 1991) and poor adaptation to inorganic N in hemlock, presumably because of damage to mycorrhizae from excess N (Gill and Lavender 1983). Salal (*Gaultheria shallon* Pursh), with ericoid mycorrhizae, is eliminated with repeated application of N fertilizer (Prescott et al. 1993). Thus species appear variably sensitive to N additions, which could influence N saturation. Podzolization or reduced biotic regulation due to a short growing season may explain high N losses observed in coastal Alaska (Stednick 1981). Nitrogen fixation inputs can sometimes far exceed atmospheric inputs (Van Miegroet and Cole 1984, Bormann et al. 1993*b*) and contribute to leaching of NO_3^- and cations in gravelly soils (Binkley et al. 1982, Van Miegroet and Cole 1984). Coastal alder stands with fine soils lose little NO_3^-, even after burning (Brown et al. 1973), and can accumulate >20 Mg N/ha (Franklin et al. 1968). In summary, these anomalous cases demonstrate that the effects of chronic N inputs on ecosystem N retention or loss is sometimes unpredictable because of our limited understanding of ecosystem processing of chronic N inputs.

Nitrogen-saturation Models for Three Ecosystem–Climate Types

The effect of climate and other site characteristics on NO_3^- leaching and other symptoms of N saturation can be illustrated by examining models that conceptualize the progression of N saturation in three different ecosystem types: New England forests, Mediterranean-climate forests in California, and high-elevation alpine ecosystems in Colorado (Fig. 1a–c). The models focus on parameters we expect to exhibit fundamental differences in response to excess N in the three ecosystem types.

New England forests

The long-term fertilization plots at Mt. Ascutney, Vermont, and at the Harvard Forest in Massachusetts and studies across an N deposition gradient in New England parallel and complement the NITREX (nitrogen saturation experiments) in Europe (Boxman et al. 1995, Emmett et al. 1995, Gundersen and Rasmussen 1995, Wright and Tietema 1995, Wright and van Breeman 1995). Several measured responses to chronic N additions were consistent across all sites (Aber et al. 1995, Magill et al. 1996, 1997). All studies showed initial and often large increases in net N mineralization. Short-term increases in N mineralization ranged from 1.3 to 4.0 times control values, but longer time responses in three of four intensive study sites showed actual decreases in net mineralization from early peak rates (Aber et al. 1995, McNulty et al. 1996, Magill et al. 1997). Only the Harvard Forest oak–maple site, which was the most N-limited initially, failed to show increased nitrification and N leaching after 8 yr of N addition treatments. The hardwood stands in the Harvard Forest have absorbed >900 kg N/ha without significant nitrification or NO_3^- leaching (Aber et al. 1995). Nitrate leaching losses were high in the Harvard Forest pine sites, and red spruce (*Picea rubens* Sarg.) at the Bear Brook site in Maine exhibited lower rates of NO_3^- assimilation into foliage and bolewood than deciduous species (Nadelhoffer et al. 1995). These findings suggest that deciduous forests may have a greater capacity for N retention and assimilation.

Waring (1987) predicted that excess available N would cause eventual conversion of boreal and subalpine coniferous forests to deciduous forest. The fertilization and N deposition gradient studies provide evidence that N saturation may lead to the conversion of slow-growing and slow N-cycling spruce–fir forests to fast growing and fast N-cycling deciduous forests (e.g., birch–maple; Fig. 1a; McNulty et al. 1996). All conifer stands showed large increases in nitrification and N leaching, and reduced growth or increased mortality. Relatively small additions of N (16–31 kg $N \cdot ha^{-1} \cdot yr^{-1}$) resulted in large reductions in biomass accumulations (McNulty et al. 1996). In the plots with the greatest mortality, high regeneration of *Betula* and *Acer* species was observed, while red spruce and balsam fir (*Abies balsamea* [L.] Mill.) did not regenerate. If this successional trend continues in the N fertilization plots, it is expected that NPP will increase as the fast-growing deciduous species enter a phase of exponential growth. Nitrate leaching and N_2O emissions will likely decrease to stage 1 levels, and net N mineralization, nitrification, and plant N uptake could be re-established at a higher equilibrium than the original spruce–fir forest. These predicted trends are a bimodal (spruce/fir decline, birch/maple regeneration) response (Fig. 1a). However, if anion and base cation leaching were to continue at high levels, cation deficiency and nutrient imbalances could prevent stand recovery. In that case, NPP would remain low, while high levels of net nitrification, NO_3^- leaching, and N_2O emissions would probably continue.

California forests

The major differences between the New England conceptual model and the California and Colorado models is the highly open nature of N processing in these western ecosystems. In California forests, nitrification, NO_3^- loss, and NO production (mainly from nitrification) are high during all stages (Fig. 1b). High nitrification rates or potential seems to be widespread in western forests (Hart and Firestone 1989, Frazer et al. 1990, Powers 1990, Covington and Sackett 1992, Davidson et al. 1992, Stark and Hart 1996), chaparral (Riggan et al. 1985, Klemmedson and Wienhold 1992, Fenn et al. 1993), and grasslands (Davidson et al. 1990), even with low N deposition rates. In California, temporal asynchrony between the major hydrologic

fluxes of NO_3^- in soil (winter and early spring) and plant and microbial N demand (presumably spring and early summer) limits plant and microbial uptake of much of the available N. However, little is known of the N immobilization potential of microbes in these systems at low temperature and high moisture availability.

We hypothesize that stage 3 (forest decline or decreased NPP) is unlikely in arid western forests, even with high N deposition and active nitrification, because soils have high base saturation and are not prone to severe acidification or Al mobilization, and because much of the available NO_3^- is leached from the rooting zone during the wet dormant season. However, stage 3 could develop if elevated N concentrations in plants and soil predispose trees to ozone injury, disease, insect infestation, drought stress, or nutrient deficiency because of reduced C allocation for root production (Perry et al. 1991, Griffin et al. 1995, Haynes and Gower 1995) as observed in high-deposition sites in the San Bernardino Mountains (N. E. Grulke and M. E. Fenn, *unpublished data*). Stage 3 may also occur if mycorrhizal development is severely hampered by excess N (Termorshuizen 1993), or if NO_3^- levels in soil solution reach phytotoxic levels (Fenn et al. 1996, Kiefer and Fenn 1997). Sensitivity to excess N has been demonstrated in ponderosa pine (Johnson et al. 1995, Griffin et al. 1996).

Zöttl (1960) and Gundersen and Rasmussen (1990) discuss four soil classifications with regard to NO_3^- production during incubation: (1) non-nitrifying soils where all soil N is NH_4^+-N; (2) nitrifying at a constant slow rate but with NH_4^+-N still dominant; (3) soil with a lag in nitrification; and (4) total nitrification, where essentially all inorganic N is NO_3^--N. The latter soils occur mainly in nutrient-rich sites. Group 4 seems to best describe the soils in California and possibly much of the arid west, where soils are of relatively high base saturation (Fig. 1b). Soils in many eastern forests are of category 3, with low levels of net nitrification generally; but with chronic N inputs, nitrification rates often increase, leading to elevated NO_3^- leaching (Aber et al. 1995). However, based on the recent findings of Stark and Hart (1996), gross nitrification rates and microbial N immobilization may be substantial in some ecosystems of groups 2 and 3.

Colorado alpine tundra

Modeling studies suggest that tundra of the Colorado Front Range is saturated with N deposition of 3.0–8.0 $kg \cdot ha^{-1} \cdot yr^{-1}$ (Baron et al. 1994, Sievering et al. 1996). Notwithstanding elevated NO_3^- leaching, alpine tundra at Niwot Ridge responded to N fertilization, and responded greatly to N and P fertilization (Bowman et al. 1995). The discrepancy between NO_3^- export from the watershed and N limitation in vegetation, is probably due to short growing seasons and a temporal disjunct between the times when most N is available (early spring) and when plants need it for growth (late spring and summer) (Baron et al. 1994). While N fertilization of tundra produced a moderate growth increase, the most dramatic response was a shift to from forb-dominated to grass-dominated communities (Bowman et al. 1993, 1995). Alpine graminoid communities have a greater capacity than forb communities to sequester N, and because of greater N use efficiency, graminoids also produce litter with lower N concentration, and probably slower decomposition rates. The production of low-quality litter may cause a negative feedback on soil N supply, thus enhancing N retention in the system (Bowman et al. 1995). Simulation results, while not specific to plant growth form, showed that the greatest response to increased N deposition consisted of large gains of organic C and N in soil (Baron et al. 1994).

We hypothesize that primary productivity in the tundra increases moderately with increased N deposition, and does so by changing community composition to favor more nitrophilous species (Fig. 1c). Large growth increases at current deposition levels are not predicted, because much of the available N from deposition and N mineralization is not available when the plants need it, due to rapid hydrologic flushing during snowmelt and short growing seasons. Additional factors such as extensive areas of exposed bedrock, steep gradients, and shallow soils limit NO_3^- retention in soil and assimilation by vegetation (Baron et al. 1994, Campbell et al. 1995*a*, *b*, Williams et al. 1996*b*).

We hypothesize that nitrification increases only modestly, partly because nitrification is common in alpine systems, even with low N deposition (Baron et al. 1994, Williams et al. 1996*b*). The insulating snow cover allows microbial processes to occur with subfreezing air temperatures. Studies by Brooks et al. (1996) and Williams et al. (1996*b*) suggest that N mineralization and nitrification are active in soils under snow, releasing N before plant N uptake begins. Nitrate export in these high-elevation catchments is a complex mix of N from atmospheric deposition that has been microbially assimilated, mineralized, and nitrified before transport to streams during snowmelt, and groundwater that is replenished from snowmelt (Williams et al. 1996*b*, Baron and Campbell 1997). A nitrogen budget from the Loch Vale Watershed showed that 80% of N lost from this alpine and subalpine watershed came from alpine zones, and of this 62% occurred during snowmelt (Baron and Campbell 1997).

Management of N-saturated Forests

In this section we discuss potential management strategies and practices as guidelines for ameliorating the symptoms of N-saturated systems. Few, if any, field studies have directly addressed or tested the efficacy of silvicultural treatments designed to improve the condition of N-saturated forests. The proposed strategies and management practices discussed are based on research and ecological principles deemed pertinent to enhancing site N retention capacity and preventing or

reducing N losses. We emphasize that application of these largely untested intensive management practices over large areas is likely to be economically and practically unfeasible. Where adequate resources are available, these strategies and practices may be developed and used to reduce the undesirable effects of N saturation. Nonetheless, in many areas the only practical long-term solution to N-saturated watersheds is to reduce atmospheric N emissions.

Historically, forest management practices have not dealt with chronic or sustained NO_3^- export from undisturbed forested watersheds. How to manage the high stores of N in soil and in the forest floor of N-rich stands is a core question. Forests at stage 1 of the N saturation model may not require management action to offset the apparently beneficial effects of increased available N—unless stand history, stand conditions, and N inputs suggest that N saturation will worsen.

Monitoring with nitrogen status indicators

Biogeochemical parameters can be used as indicators for monitoring forest N status (Fenn and Poth 1997). Suggested indicators are those that commonly respond to excess N in a wide range of ecosystem types and include: foliar N : nutrient ratios (N:P, N : cation), foliar NO_3^-, foliar $\delta^{15}N$ and arginine concentration (Näsholm et al. 1997), soil C:N ratio, NO_3^- in soil extracts or in soil solution, and flux rates of nitrogenous trace gases from soil (Fenn and Poth 1997). Seasonal patterns of streamwater NO_3^- concentration are an especially good indicator of watershed N status (Stoddard 1994).

Potential management practices

We recommend treatments in N-saturated forests or watersheds that focus on strategies to maximize N retention and avoid stand characteristics that may be causally related to the symptoms of N saturation.

Stand development objectives.—In areas with high risk of N saturation, it is desirable to avoid excess maturation of the stand, since forests that are no longer increasing in total biomass and accumulating nutrients will be more prone to export N. Decreasing the stand component of N_2-fixing species such as alder or locust is an option for reducing N inputs. If species decline results from N saturation, the forest may be regenerated with more N-demanding species (McNulty et al. 1996: Fig. 2a)—a gradual self-correcting mechanism for conserving nitrogen. Aber et al. (1991) suggested that altering species composition from higher to lower N use efficiency may delay the onset of N saturation by increasing the N-cycling potential of the system.

A number of studies have found a strong association between stand age or developmental stage and N retention capacity (Vitousek and Reiners 1975, Peet 1992, Emmett et al. 1993, Reynolds et al. 1994). Silvicultural treatments that maintain vigorous forest growth (e.g., selective harvesting, replanting, thinning, and fertilization) are likely to aid in retaining N more effectively as N is incorporated into plant biomass, and as higher stand evapotranspiration reduces streamwater discharge and nutrient losses from the watershed (Swank 1988). The formation of forest gaps may increase NO_3^- leaching for a few years because plant uptake will be reduced and nitrification increased in gaps due to warmer temperatures and reduced competition for available N (Edwards and Helvey 1991). When vegetation regenerates in the gaps, NO_3^- losses should decrease.

Harvest intensity.—Whole tree harvesting results in lower NO_3^- leachate losses than does conventional harvesting, where branches and foliage (slash) are left on site (Hendrickson et al. 1989, Stevens and Hornung 1990, Lundborg 1997). Harvest intensity will probably have the most profound effect on N leaching losses during the first several years immediately after the harvest (Likens et al. 1978). Rosén and Lundmark-Thelin (1987) demonstrated that large quantities of dissolved organic N are leached from slash and that inorganic N concentrations are high in soil under slash piles. Nitrate losses after whole-tree harvesting are also reduced compared to conventional harvesting because slash removal allows for more rapid regeneration of vegetation cover, resulting in greater vegetative N demand and N retention (Stevens and Hornung 1990, Staaf and Olsson 1994, Lundborg 1997). Harvesting can be beneficial in managing excess N in unforested ecosystems as well. Annual summer harvesting of hay from Dutch fens with high N deposition removes enough N to prevent eutrophication of the system (Verhoeven et al. 1996). This strategy could exacerbate N saturation in places where cations or other nutrients are deficient (Aber et al. 1991), requiring fertilization with limiting nutrients.

Fertilization and liming.—Fertilizing with P or other nutrients that may become growth limiting with excess N (Mohren et al. 1986, Houdijk and Roelofs 1993) could enhance the N uptake capacity of the stand. Fertilization of a 45-yr-old Sitka spruce plantation in north Wales with P and K substantially reduced NO_3^- concentrations in soilwater. Increased N uptake by the trees was approximately equal to NO_3^- leaching in the unfertilized areas, suggesting that alleviating P and K deficiency increased N uptake (Stevens et al. 1993). Glatzel (1990) concluded that the N storage capacity of forest soils may be managed by optimal tree species selection and by improving the base status of soils by liming and fertilization. However, some studies indicate that liming increases net nitrification rates and NO_3^- leaching, probably as a result of more favorable soil pH values after liming (Marschner et al. 1989, Deboer et al. 1993, Brahmer 1994).

Riparian ecotones.—Riparian ecotones can be highly effective in removing N and P in runoff from agricultural watersheds (Lowrance et al. 1984, Peterjohn and Correll 1984). Buffer strips of riparian vegetation could also be managed for maximum nutrient retention in N-saturated wildland watersheds, thus protecting

streamwater quality (Hanson et al. 1994). The first 5 m of riparian forest soils that are transitional between uplands and wetlands were especially effective in removing NO_3^- in the southeastern U.S. coastal plain and in Great Britain (Lowrance 1992, Haycock and Pinay 1993). In several studies, buffer strips 5–30 m in width have been shown to be highly effective in nutrient retention from surface runoff and in subsurface flow (Haycock et al. 1993, Vought et al. 1994, Risser 1995).

Haycock et al. (1993) provide a conceptual framework for riparian management strategies to reduce N loss to surface waters. Increased complexity of the riparian vegetation maximizes vegetative N uptake, which dominates N retention in the summer. Riparian vegetation also supplies the necessary C for denitrification, which is usually the principal process for removing excess N from water during the dormant season (Haycock et al. 1993). Riparian ecotones may function as short- and long-term nutrient filters and sinks if trees are harvested periodically to ensure a net uptake of nutrients (Lowrance et al. 1984). Wetlands can also function as strong N sinks, and restoration or creation of wetlands has been proposed as a management tool for reducing N in surface waters (Fleischer et al. 1991). However, favoring N inputs into wetlands is likely to increase N_2O emissions.

Prescribed fire.—Prescribed fire is an unorthodox method for reducing the effects of excess N, yet along with numerous other benefits, it has been suggested as a possible management tool where N deposition and streamwater NO_3^- concentrations are very high in chaparral ecosystems near Los Angeles, California (Riggan et al., 1994). Fire suppression has contributed to the development of N saturation in fire-adapted ecosystems in southern California by allowing N to accumulate in soil and the forest floor (Riggan et al. 1985, Fenn et al. 1996). Implementing prescribed fire in N-saturated, fire-adapted ecosystems will: (1) release N from the system, and (2) prepare a seedbed for regeneration of seedlings or induce resprouting of shrubs that will later be much stronger N sinks than decadent vegetation. Burning will initially cause a strong pulse of released N previously immobilized in vegetation, detritus, and soil organic matter. A fraction of the released N will be volatilized, while NH_4^+ released will likely be nitrified after the fire and result in leached NO_3^- (Dunn et al. 1979, Riggan et al. 1994). Concentrations of NO_3^- in burned watersheds return to background levels faster than other ions, commonly within 2–3 yr (Bayley and Schindler 1991). Prescribed burning or the application of wood ash to the forest floor can stimulate nitrification, presumably by increasing soil pH (Martikainen 1984), by supplying nutrients such as Ca or K, or by reducing competition between autotrophic nitrifiers and heterotrophs (Pietikäinen and Fritze 1995). But in the long run, prescribed fire repeated at regular intervals will likely reduce NO_3^- export in streamwater.

Policy and regulatory action

Increasing trends in N deposition (Galloway et al. 1994) suggest that the geographic scope of N-saturated ecosystems will also increase. Sustainability of N-saturated forests, water quality protection, and effects on biota of surface waters and coastal marine ecosystems are major concerns and constitute active areas of research. National parks and wilderness areas with chronic N deposition are often highly prone to N saturation because of stand maturity, accumulation of N in soil, and (particularly in high-elevation sites) low N retention capacity of soils and vegetation. Yet management options are limited in these protected areas. These factors suggest that strategic reductions in N emissions are needed, as well as research on management practices for alleviating the effects of N excess.

Research Needs

The greatest remaining challenge in the study of N saturation of forests is to understand the mechanisms by which large amounts of N are incorporated into forest soils, and to develop a method for predicting N retention capacity. Predicting the N status of impacted forests will require greater quantitative information on the kinetics, capacity, and controlling factors of the processes regulating N retention and release. We need more data on the relative rates of abiotic vs. biotic N retention and incorporation in soil. Related questions include: How is microbially assimilated N transferred to the stable soil humus pool? What is the role of microbes in retaining N, especially when hydrologic flows transport NO_3^- through the soil while vegetation is dormant (e.g., under snow layers and during snowmelt) or when vegetation has low affinity for NO_3^- (Rothstein et al. 1996)? Are nitrification and microbial assimilation of NO_3^- widespread in eastern hardwoods and other forest types, as reported for western coniferous forests (Stark and Hart 1996)?

Additional pertinent research questions include: What are the best indicators of N saturation? How can large N stores in soil and the forest floor best be managed? What is the relative importance of inputs and outputs of dissolved organic N and dissolved inorganic N in different systems? Are greater cumulative inputs of N required to induce N saturation in deciduous forests than in evergreen forests? Does the lack of reduced growth rates in deciduous stands receiving chronic N inputs mean that N saturation does not pose a problem for forest health in these forest types, or only that higher N retention rates will allow a delay in the onset of decline? Does chronic N deposition play a significant role in spruce decline across the northeastern United States? What are the effects of N saturation on mycorrhizal development in different forest types? How does N excess affect plant susceptibility to other abiotic (drought, ozone, cold tolerance) and biotic (pests and pathogens) stresses? What are the mechanisms and how

widespread is the observed N inhibition of litter decomposition? Will regional N deposition patterns be affected by increased global emissions of N?

Conclusions

Most forests in the northern hemisphere remain N limited, and increasing N deposition will generally cause a growth increase, even in Europe (Kauppi et al. 1992, Eriksson and Johansson 1993, Binkley and Högberg 1997), where deposition levels are generally higher than in North America (Lindberg et al. 1990). Intensively harvested or short-rotation forests are unlikely to become N saturated, even at the highest deposition levels. There are, however, increasing reports of forests that are N saturated. The focus of this paper is upon such forests, although we do not wish to imply that all forests will become N saturated or that N saturation is as yet a widespread catastrophic problem. Even so, chronic inputs of fixed N over vast acreages of terrestrial and aquatic ecosystems demand our attention, especially considering the unique role of N in biotic systems. Until recently, research into N cycling was predominantly concerned with alleviating N limitation in production agriculture and forestry, or with understanding biotic responses to limited N resources. The phenomenon of N saturation presents a new paradigm of ecosystem function wherein N is frequently in excess of biotic demand. Many questions remain unanswered about the long-term ecological sustainability of N-saturated systems, and of the mechanisms, forms, and controlling factors of N retention.

Nitrogen saturation conditions have been documented in a variety of ecosystem types in eastern and western North America. Geographic patterns in streamwater export of NO_3^- generally parallel patterns of N deposition but do not alone identify ecosystems at risk. Nitrogen saturation is also a function of physical factors (climate, geology, topography, soils), biological factors (vegetation type, successional stage, stand condition), and human factors (land use and management, N emissions). These factors will need to be evaluated for a wide range of ecosystems (e.g., tundra, forests, chaparral, grasslands, estuaries) to identify resources at risk, such as water quality, forest productivity and sustainability, threatened or endangered species, and aquatic biota. The chemical environment of freshwater and estuarine ecosystems is largely driven by processes that occur on terrestrial watersheds. Nitrogen saturation of watersheds is an important N source contributing to eutrophication of estuaries.

Plant succession patterns and biodiversity are significantly affected by chronic N additions in some systems. The hydrological patterns of ecosystems are major drivers of N transport within the watershed and exert major control on N-cycling processes at all scales. Field studies and simulation models indicate feedback mechanisms between N deposition and the global balance of greenhouse gases. Current evidence indicates that N deposition increases carbon storage in woody biomass and decreases the rate of carbon release in the later stages of organic matter decomposition. However, emissions of nitrogenous trace gases from soil increase with N availability, while consumption of CH_4 generally decreases with greater available N. Although N-saturated forests export high levels of NO_3^-, they simultaneously accumulate N, often retaining >85% of inorganic N. Disturbances such as fire, pest outbreaks, or harvest activities trigger massive N releases from these systems.

The goal of research should be to increase our understanding of the mechanisms of N retention and release, and increase our ability to mitigate the undesirable consequences of N saturation in upland terrestrial systems and in aquatic systems receiving the chemical outputs of these watersheds. Nitrogen emissions are projected to increase greatly in underdeveloped countries in the next few decades. The incidence of N-saturated ecosystems and environmental impacts are also expected to increase.

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Literature Cited

Aber, J. D. 1992. Nitrogen cycling and nitrogen saturation in temperate forest ecosystems. Trends in Ecology and Evolution **7**:220–223.

Aber, J. D., A. Magill, S. G. McNulty, R. D. Boone, K. J. Nadelhoffer, M. Downs, and R. Hallett. 1995. Forest biogeochemistry and primary production altered by nitrogen saturation. Water, Air and Soil Pollution **85**:1665–1670.

Aber, J. D., J. M. Melillo, K. J. Nadelhoffer, J. Pastor, and R. D. Boone. 1991. Factors controlling nitrogen cycling and nitrogen saturation in northern temperate forest ecosystems. Ecological Applications **1**:303–315.

Aber, J. D., K. J. Nadelhoffer, P. Steudler, and J. M. Melillo. 1989. Nitrogen saturation in northern forest ecosystems. BioScience **39**:378–386.

Adams, M. B., T. R. Angradi, and J. N. Kochenderfer. 1997. Stream water and soil solution responses to 5 years of nitrogen and sulfur additions at the Fernow Experimental Forest, West Virginia. Forest Ecology and Management **95**: 79–91.

Adams, M. B., P. J. Edwards, F. Wood, and J. N. Kochenderfer. 1993. Artificial watershed acidification on the Fernow Experimental Forest, USA. Journal of Hydrology **150**:505–519.

Adams, M. B., J. N. Kochenderfer, F. Wood, T. R. Angradi, and P. Edwards. 1994. Forty years of hydrometeorological data from the Fernow Experimental Forest, West Virginia. General Technical Report NE-184. USDA Forest Service, Northeastern Forest Experiment Station, Radnor, Pennsylvania, USA.

Ågren, G. I., and E. Bosatta. 1988. Nitrogen saturation of terrestrial ecosystems. Environmental Pollution **54**:185–197.

Anderson, I. C., J. S. Levine, M. A. Poth, and P. J. Riggan. 1988. Enhanced biogenic emissions of nitric oxide and nitrous oxide following surface biomass burning. Journal of Geophysical Research **93**:3893–3898.

Attiwill, P. M., and M. A. Adams. 1993. Tansley review number 50. Nutrient cycling in forests. New Phytologist **124**:561–582.

Bååth, E., B. Lundgren, and B. Söderström. 1981. Effects of nitrogen fertilization on the activity and biomass of fungi and bacteria in a podzolic soil. Zentralblatt für Bakteriologie, Mikrobiologie und Hygiene, Originale 1 Abteilung **C2**:90–98.

Baker, J. P., et al. 1996. Episodic acidification of small streams in the northeastern United States: effects on fish populations. Ecological Applications **6**:422–437.

Baron, J. S., and D. H. Campbell. 1997. Nitrogen fluxes in a high elevation Colorado Rocky Mountain basin. Hydrological Processes **11**:783–799.

Baron, J. S., D. S. Ojima, E. A. Holland, and W. J. Parton. 1994. Analysis of nitrogen saturation potential in Rocky Mountain tundra and forest: implications for aquatic systems. Biogeochemistry **27**:61–82.

Bayley, S. E., and D. W. Schindler. 1991. The role of fire in determining stream water chemistry in northern coniferous forests. Pages 141–165 *in* H. A. Mooney, E. Medina, D. W. Schindler, E.-D. Schulze, and B. H. Walker, editors. Ecosystem experiments. Scope 45. John Wiley and Sons, Chichester, UK.

Berg, B., G. Ekbohm, and C. McClaugherty. 1984. Lignin and holocellulose relations during decomposition in a Scots pine forest. Canadian Journal of Botany **62**:2540–2550.

Berg, B., and C. McClaugherty. 1987. Nitrogen release from litter in relation to disappearance of lignin. Biogeochemistry **4**:219–224.

Berg, B., C. McClaugherty, A. Virzo de Santo, M. B. Johansson, and G. Ekbohm. 1995. Decomposition of litter and soil organic matter: Can we distinguish a mechanism for soil organic matter buildup? Scandinavian Journal of Forest Research **10**:108–119.

Berg, B., H. Staaf, and B. Wessen. 1987. Decomposition and nutrient release in needle litter from nitrogen-fertilized Scots pine (*Pinus sylvestris*) stands. Scandinavian Journal of Forest Research **2**:399–415.

Billings, W. D., K. M. Peterson, J. O. Luken, and D. A. Mortensen. 1984. Interaction of increasing atmospheric carbon dioxide and soil nitrogen on the carbon balance of tundra microcosms. Oecologia **65**:26–29.

Binkley, D., and P. Högberg. 1997. Does atmospheric deposition of nitrogen threaten Swedish forests? Forest Ecology and Management **92**:119–152.

Binkley, D., J. P. Kimmins, and M. C. Feller. 1982. Water chemistry profiles in an early- and a mid-successional forest in Coastal British Columbia. Canadian Journal of Forest Research **12**:240–248.

Blew, R. D., and R. L. Edmonds. 1996. Reply to discussion by Gordon W. Stuart: "Biogeochemistry of an old-growth forested watershed, Olympic National Park, Washington." Water Resources Bulletin **32**:409–410.

Böhm, M. 1992. Air quality and deposition. Pages 63–152 *in* R. K. Olson, D. Binkley, and M. Böhm, editors. The response of western forests to air pollution. Ecological Studies 97. Springer-Verlag, New York, New York, USA.

Bormann, B. T., F. H. Bormann, W. B. Bowden, R. S. Pierce, S. P. Hamburg, D. Wang, M. C. Snyder, C. Y. Li, and R. C. Ingersoll. 1993*a*. Rapid N_2 fixation in pines, alder, and locust: evidence from the sandbox ecosystem study. Ecology **74**:583–598.

Bormann, B. T., K. Cromack, Jr., and W. O. Russell, III. 1993*b*. Influences of alder on soils and long-term ecosystem productivity. *In* D. Hibbs, D. S. DeBell, and R. F. Tarrant, editors. Biology and management of alder. Oregon State University Press, Corvallis, Oregon, USA.

Bormann, B. T., R. F. Tarrant, M. C. McClellan, and T. Savage. 1989. Chemistry of rain and cloud water at remote sites in Alaska and Oregon. Journal of Environmental Quality **18**:149–152.

Bowden, W. B., and F. H. Bormann. 1986. Transport and loss of nitrous oxide in soil water after forest clear-cutting. Science **233**:867–869.

Bowman, W. D., T. A. Theodose, and M. C. Fisk. 1995. Physiological and production responses of plant growth forms to increases in limiting resources in alpine tundra: implications for differential community response to environmental change. Oecologia **101**:217–227.

Bowman, W. D., T. A. Theodose, J. C. Schardt, and R. T. Conant. 1993. Constraints of nutrient availability on primary production in two alpine tundra communities. Ecology **74**:2085–2097.

Boxman, A. W., D. van Dam, H. F. G. Van Dijk, R. F. Hogervorst, and C. J. Koopmans. 1995. Ecosystem responses to reduced nitrogen and sulphur inputs into two coniferous stands in The Netherlands. Forest Ecology and Management **71**:7–29.

Brahmer, G. 1994. Effects of whole catchment liming and Mg addition on soil water and runoff at two forested watersheds in the Black Forest (Germany). Forest Ecology and Management **68**:47–60.

Bray, J. R., and E. Gorham. 1964. Litter production in forests of the world. Advances in Ecological Research **2**:101–157.

Bronson, K. F., and A. R. Mosier. 1993. Effect of nitrogen fertilizer and nitrification inhibitors on methane and nitrous oxide fluxes in irrigated corn. Pages 369–386 *in* R. S. Oremland, editor. Biogeochemistry of global change: radiatively active trace gases. Chapman and Hall, New York, New York, USA.

Brooks, P. D., M. W. Williams, and S. K. Schmidt. 1996. Microbial activity under alpine snowpacks, Niwot Ridge, Colorado. Biogeochemistry **32**:93–113.

Brown, G. W., A. R. Gahler, and R. B. Marston. 1973. Nutrient losses after clear-cut logging and slash burning in the Oregon Coast Range. Water Resources Research **9**:1450–1453.

Buchmann, N., G. Gebauer, and E.-D. Schulze. 1996. Partitioning of ^{15}N-labeled ammonium and nitrate among soil, litter, below- and above-ground biomass of trees and understory in a 15-year-old *Picea abies* plantation. Biogeochemistry **33**:1–23.

Bytnerowicz, A., and M. E. Fenn. 1996. Nitrogen deposition in California forests: a review. Environmental Pollution **92**: 127–146.

Campbell, D. H., D. W. Clow, G. P. Ingersoll, M. A. Mast, N. E. Spahr, and J. T. Turk. 1995*a*. Nitrogen deposition and release in alpine watersheds, Loch Vale, Colorado, USA. Pages 243–253 *in* K. A. Tonnessen, M. W. Williams, and M. Tranter, editors. Proceedings: Biogeochemistry of Seasonally Snow-covered Catchments. XXI Assembly of the International Union of Geodesy and Geophysics, Boulder, Colorado, USA.

Campbell, D. H., D. W. Clow, G. P. Ingersoll, M. A. Mast, N. E. Spahr, and J. T. Turk. 1995*b*. Processes controlling the chemistry of two snowmelt-dominated streams in the Rocky Mountains. Water Resources Research **31**:2811–2821.

Castro, M. S., W. T. Peterjohn, J. M. Melillo, and P. A. Steudler. 1994. Effects of nitrogen fertilization on the fluxes of N_2O, CH_4, and CO_2 from soils in a Florida slash pine plantation. Canadian Journal of Forest Research **24**:9–13.

Castro, M. S., P. A. Steudler, J. M. Melillo, J. D. Aber, and R. D. Bowden. 1995. Factors controlling atmospheric methane consumption by temperate forest soils. Global Biogeochemical Cycles **9**:1–10.

Cheng, H. H., and L. T. Kurtz. 1963. Chemical distribution of added nitrogen in soils. Soil Science Society of America Proceedings **27**:312–316.

Cheng, W. X., Q. L. Zhang, D. C. Coleman, C. R. Carroll, and C. A. Hoffman. 1996. Is available carbon limiting microbial respiration in the rhizosphere? Soil Biology and Biochemistry **28**:1283–1288.

Chorover, J., P. M. Vitousek, D. A. Everson, A. M. Esperanza, and D. Turner. 1994. Solution chemistry profiles of mixed-conifer forests before and after fire. Biogeochemistry **26**: 115–44.

Cole, D. W., H. Van Miegroet, and N. W. Foster. 1992. Retention or loss of N in IFS sites and evaluation of relative importance of processes. Pages 196–199 *in* D. W. Johnson and S. E. Lindberg, editors. Atmospheric deposition and forest nutrient cycling. Ecological Studies 91. Springer-Verlag, New York, New York, USA.

Cole, D. W., and M. Rapp. 1981. Elemental cycling in forest ecosystems. Pages 341–409 *in* D. E. Reichle, editor. Dynamic properties of forest ecosystems. Cambridge University Press, London, UK.

Covington, W. W., and S. S. Sackett. 1992. Soil mineral nitrogen changes following prescribed burning in ponderosa pine. Forest Ecology and Management **54**:175–191.

Cromack, K., Jr. 1973. Litter production and decomposition in a mixed hardwood watershed and in a white pine watershed at Coweeta Hydrologic Station, North Carolina. Dissertation. University of Georgia, Athens, Georgia, USA.

Cronan, C. S., and D. F. Grigal. 1995. Use of calcium/aluminum ratios as indicators of stress in forest ecosystems. Journal of Environmental Quality **24**:209–226.

Dahlgren, R. A. 1994. Soil acidification and nitrogen saturation from weathering of ammonium-bearing rock. Nature **368**:838–841.

Davidson, E. A. 1992. Sources of nitric oxide and nitrous oxide following wetting of dry soil. Soil Science Society of America Journal **56**:95–102.

———. 1993. Soil water content and the ratio of nitrous oxide to nitric oxide emitted from soil. Pages 369–386 *in* R. S. Oremland, editor. Biogeochemistry of global change: radiatively active trace gases. Chapman and Hall, New York, New York, USA.

Davidson, E. A., S. C. Hart, and M. K. Firestone. 1992. Internal cycling of nitrate in soils of a mature coniferous forest. Ecology **73**:1148–1156.

Davidson, E. A., J. M. Stark, and M. K. Firestone. 1990. Microbial production and consumption of nitrate in an annual grassland. Ecology **71**:1968–1975.

Davidson, E. A., and W. T. Swank. 1990. Nitrous oxide dissolved in soil solution: an insignificant pathway of nitrogen loss from a southeastern hardwood forest. Water Resources Research **26**:1687–1690.

Deboer, W., M. P. J. Hundscheid, J. M. T. Schotman, S. R. Troelstra, and H. J. Laanbroek. 1993. In situ net N-transformations in pine, fir, and oak stands of different ages on acid sandy soil, 3 years after liming. Biology and Fertility of Soils **15**:120–126.

Dillon, P. J., and L. A. Molot. 1990. The role of ammonium and nitrate retention in the acidification of lakes and forested catchments. Biogeochemistry **11**:23–44.

Dise, N. B., and R. F. Wright. 1995. Nitrogen leaching from European forests in relation to nitrogen deposition. Forest Ecology and Management **71**:153–161.

Dow, C. L., and D. R. DeWalle. 1997. Sulfur and nitrogen budgets for five forested Appalachian Plateau basins. Hydrological Processes **11**:801–816.

Driscoll, C. T., R. M. Newton, C. P. Gubala, J. P. Baker, and S. W. Christensen. 1991. Adirondack Mountains. Pages 133–202 *in* D. F. Charles, editor. Acidic deposition and aquatic ecosystems. Springer-Verlag, New York, New York, USA.

Driscoll, C. T., and R. Van Dreason. 1993. Seasonal and long-term temporal patterns in the chemistry of Adirondack lakes. Water, Air and Soil Pollution **67**:319–344.

Duckworth, C. M. S., and M. S. Cresser. 1991. Factors influencing nitrogen retention in forest soils. Environmental Pollution **72**:1–21.

Dunn, P. H., L. F. De Bano, and G. E. Eberlein. 1979. Effects of burning chaparral soils. II. Soil microbes and nitrogen mineralization. Soil Science Society of America Journal **43**:509–514.

Edfast, A.-B., T. Näsholm, and A. Ericsson. 1990. Free amino acid concentrations in needles of Norway spruce and Scots pine trees on different sites in areas with two levels of nitrogen deposition. Canadian Journal of Forest Research **20**:1132–1136.

Edmonds, R. L., T. B. Thomas, and R. D. Blew. 1995. Biogeochemistry of an old-growth forested watershed, Olympic National Park, Washington. Water Resources Bulletin **31**:409–419.

Edwards, P. M., and J. D. Helvey. 1991. Long-term ionic increases from a central Appalachian forested watershed. Journal of Environmental Quality **20**:250–255.

Eldridge, D. J., and R. S. B. Greene. 1994. Microbiotic soil crusts—a review of their roles in soil and ecological processes in the rangelands of Australia. Australian Journal of Soil Research **32**:389–415.

Emmett, B. A., S. A. Brittain, S. Hughes, J. Gorres, V. Kennedy, D. Norris, R. Rafarel, B. Reynolds, and P. A. Stevens. 1995. Nitrogen addition ($NaNO_3$ and NH_4NO_3) at Aber forest, Wales. I. Response of throughfall and soil water chemistry. Forest Ecology and Management **71**:45–59.

Emmett, B. A., B. Reynolds, P. A. Stevens, D. A. Norris, S. Hughes, J. Görres, and I. Lubrecht. 1993. Nitrate leaching from afforested Welsh catchments: interactions between stand age and nitrogen deposition. Ambio **22**:386–394.

Ericsson, A., L. G. Norden, T. Nasholm, and M. Walheim. 1993. Mineral nutrient imbalances and arginine concentrations in needles of *Picea abies* (L.) Karst from two areas with different levels of airborne deposition. Trees **8**:67–74.

Eriksson, H., and U. Johansson. 1993. Yields of Norway spruce (*Picea abies* (L.) Karst.) in two consecutive rotations in southwestern Sweden. Plant and Soil **154**:239–247.

Evans, R. D., and J. R. Ehleringer. 1993. A break in the nitrogen cycle in aridlands: evidence from $\delta^{15}N$ of soils. Oecologia **94**:314–317.

Federer, C. A., J. W. Hornbeck, L. M. Tritton, C. W. Martin, R. S. Pierce, and C. T. Smith. 1989. Long-term depletion of calcium and other nutrients in eastern U.S. forests. Environmental Management **13**:593–601.

Feger, K. H. 1992. Nitrogen cycling in two Norway spruce (*Picea abies*) ecosystems and effects of a $(NH_4)_2SO_4$ addition. Water, Air and Soil Pollution **61**:295–307.

Fenn, M. E., and M. A. Poth. 1997. Indicators of nitrogen status in California forests. *In* A. Bytnerowicz, editor. Proceedings: Air Pollution and Climate Change Effects on Forest Ecosystems. 5–9 February 1996, Riverside, California. USDA Forest Service, Pacific Southwest Research Station, Albany, California, USA. ⟨http://www.rfl.pswfs.gov/pubs/psw-gtr-164/index.html⟩

Fenn, M. E., M. A. Poth, P. H. Dunn, and S. C. Barro. 1993. Microbial N and biomass, respiration and N mineralization in soils beneath two chaparral species along a fire-induced age gradient. Soil Biology and Biochemistry **25**:457–466.

Fenn, M. E., M. A. Poth, and D. W. Johnson. 1996. Evidence for nitrogen saturation in the San Bernardino Mountains in southern California. Forest Ecology and Management **82**: 211–230.

Fisher, D. C., and M. Oppenheimer. 1991. Atmospheric nitrogen deposition and the Chesapeake Bay Estuary. Ambio **20**:102–108.

Flanagan, P. W., and K. Van Cleve. 1983. Nutrient cycling

in relation to decomposition and organic-matter quality in taiga ecosystems. Canadian Journal of Forest Research **13**: 795–817.

Fleischer, S., L. Stibe, and L. Leonardson. 1991. Restoration of wetlands as a means of reducing nitrogen transport to coastal waters. Ambio **20**:271–272.

Flum, T., and S. C. Nodvin. 1995. Factors affecting streamwater chemistry in the Great Smoky Mountains, USA. Water, Air and Soil Pollution **85**:1707–1712.

Fog, K. 1988. The effect of added nitrogen on the rate of decomposition of organic matter. Biological Reviews **63**: 433–462.

Foster, N. W., E. G. Beauchamp, and C. T. Corke. 1980. Microbial activity in *Pinus banksiana* Lamb. forest floor amended with nitrogen and carbon. Canadian Journal of Soil Science **60**:199–209.

Foster, N. W., P. W. Hazlett, J. A. Nicolson, and I. K. Morrison. 1989*a*. Ion leaching from a sugar maple forest in response to acidic deposition and nitrification. Water, Air and Soil Pollution **48**:251–261.

Foster, N. W., J. A. Nicolson, and P. W. Hazlett. 1989*b*. Temporal variation in nitrate and nutrient cations in drainage waters from a deciduous forest. Journal of Environmental Quality **18**:238–244.

Franklin, J. F., C. T. Dyrness, D. G. Moore, and R. F. Tarrant. 1968. Chemical soil properties under coastal Oregon stands of alder and conifers. Pages 157–172 *in* J. M. Trappe et al., editors. Biology of alder. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon, USA.

Frazer, D. W., J. G. McColl, and R. F. Powers. 1990. Soil nitrogen mineralization in a clearcutting chronosequence in a northern California conifer forest. Soil Science Society of America Journal **54**:1145–1152.

Friedland, A. J., G. J. Hawley, and G. A. Gregory. 1988. Red spruce (*Picea rubens* Sarg.) foliar chemistry in Vermont and northern New York. Plant and Soil **105**:189–193.

Galloway, J. N. 1995. Acid deposition: perspectives in time and space. Water, Air and Soil Pollution **85**:15–24.

Galloway, J. N., H. Levy II, and P. S. Kasibhatla. 1994. Year 2020: consequences of population growth and development on deposition of oxidized nitrogen. Ambio **23**:120–123.

Gerloff, G. C., D. G. Moore, and J. T. Curtis. 1966. Selective absorption of mineral elements by native plants of Wisconsin. Plant and Soil **25**:393–405.

Gill, R. and D. P. Lavender. 1983. Urea fertilization: effects on primary root mortality and mycorrhizal development of young-growth western hemlock. Forest Science **29**:751–760.

Gilliam, F. S., M. B. Adams, and B. M. Yurish. 1996. Ecosystem nutrient responses to chronic nitrogen inputs at Fernow Experimental Forest, West Virginia. Canadian Journal of Forest Research **26**:196–205.

Glatzel, G. 1990. The nitrogen status of Austrian forest ecosystems as influenced by atmospheric deposition, biomass harvesting and lateral organomass exchange. Plant and Soil **128**:67–74.

Gorham, E., P. M. Vitousek, and W. A. Reiners. 1979. The regulation of chemical budgets over the course of terrestrial ecosystem succession. Annual Review of Ecology and Systematics **10**:53–84.

Griffin, K. L., W. E. Winner, and B. R. Strain. 1995. Growth and dry matter partitioning in loblolly and ponderosa pine seedlings in response to carbon and nitrogen availability. New Phytologist **129**:547–556.

Griffin, K. L., J. T. Ball, and B. R. Strain. 1996. Direct and indirect effects of elevated CO_2 on whole-shoot respiration in ponderosa pine seedlings. Tree Physiology **16**:33–41.

Gundersen, P., and L. Rasmussen. 1990. Nitrification in forest soils: effects from nitrogen deposition on soil acidification and aluminum release. Reviews of Environmental Contamination and Technology **113**:1–45.

Gundersen, P., and L. Rasmussen. 1995. Nitrogen mobility in a nitrogen limited forest at Klosterhede, Denmark, examined by NH_4NO_3 addition. Forest Ecology and Management **71**:75–88.

Hanson, G. C., P. M. Groffman, and A. J. Gold. 1994. Symptoms of nitrogen saturation in a riparian wetland. Ecological Applications **4**:750–756.

Harmon, M. E. 1992. Long-term experiments on log decomposition at the H. J. Andrews Experimental Forest. General Technical Report PNW-GTR-280. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA

Harmon, M. E., et al. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research **15**:133–302.

Harmon, M. E., J. Sexton, B. A. Caldwell, and S. E. Carpenter. 1994. Fungal sporocarp mediated losses of Ca, Fe, K, Mg, Mn, N, P, and Zn from conifer logs in the early stages of decomposition. Canadian Journal of Forest Research **24**: 1883–1893.

Harr, R. D. 1982. Fog drip in the Bull Run Municipal Watershed, Oregon. Water Resources Bulletin **18**:785–789.

Hart, S. C., and M. K. Firestone. 1989. Evaluation of three *in situ* soil nitrogen availability assays. Canadian Journal of Forest Research **19**:185–191.

Hart, S. C., M. K. Firestone, E. A. Paul, and J. L. Smith. 1993. Flow and fate of soil nitrogen in an annual grassland and a young mixed-conifer forest. Soil Biology and Biochemistry **25**:431–442.

Haycock, N. E., and G. Pinay. 1993. Groundwater nitrate dynamics in grass and poplar vegetated riparian buffer strips during the winter. Journal of Environmental Quality **22**:273–278.

Haycock, N. E., G. Pinay, and C. Walker. 1993. Nitrogen retention in river corridors: European perspective. Ambio **22**:340–346.

Haynes, B. E., and S. T. Gower. 1995. Belowground carbon allocation in unfertilized and fertilized red pine plantations in northern Wisconsin. Tree Physiology **15**:317–325.

Haynes, R. J. 1986. The decomposition process: mineralization, immobilization, humus formation, and degradation. Pages 52–109 *in* T. T. Kozlowski, editor. Mineral nitrogen in the plant–soil system. Harcourt Brace Jovanovich, Orlando, Florida, USA.

Hedin, L. O., J. J. Armesto, and A. H. Johnson. 1995. Patterns of nutrient loss from unpolluted, old-growth temperate forests: evaluation of biogeochemical theory. Ecology **76**:493–509.

Heilman, P. E., and S. P. Gessel. 1963. Nitrogen requirements and the biological cycling of nitrogen in Douglas-fir stands in relationship to the effects of nitrogen fertilization. Plant and Soil **18**:386–402.

Hendrickson, O. Q., L. Chatarpaul, and D. Burgess. 1989. Nutrient cycling following whole-tree and conventional harvest in northern mixed forest. Canadian Journal of Forest Research **19**:725–735.

Hill, A. R. 1993. Nitrogen dynamics of storm runoff in the riparian zone of a forested watershed. Biogeochemistry **20**: 19–44.

Hinga, K. R., A. A. Keller, and C. A. Oviatt. 1991. Atmospheric deposition and nitrogen inputs to coastal waters. Ambio **20**:256–260.

Hornbeck, J. W., S. W. Bailey, D. C. Buso, and J. B. Shanley. 1997. Streamwater chemistry and nutrient budgets for forested watersheds in New England: variability and management implications. Forest Ecology and Management **93**: 73–89.

Houdijk, A. L. F., and J. G. M. Roelofs. 1993. The effects

of atmospheric nitrogen deposition and soil chemistry on the nutritional status of *Pseudotsuga menziesii, Pinus nigra* and *Pinus sylvestris*. Environmental Pollution **80**:79–84.

Howarth, R. W. 1988. Nutrient limitation of net primary production in marine ecosystems. Annual Review of Ecology **19**:89–110.

Howarth, R. W., et al. 1996. Regional nitrogen budgets and riverine N and P fluxes for the drainages to the North Atlantic Ocean: natural and human influences. Biogeochemistry **35**:75–139.

Hungate, B. A., T. E. Jordan, R. B. Jackson, and B. G. Drake. 1997. Atmospheric nitrogen deposition. Science **275**:739–740.

Hunt, H. W., E. R. Ingham, D. C. Coleman, E. T. Elliott, and C. P. P. Reid. 1988. Nitrogen limitation of production and decomposition in prairie, mountain meadow, and pine forest. Ecology **69**:1009–1016.

Ingersoll, C. G., D. D. Gulley, D. R. Mount, M. E. Mueller, J. D. Fernandez, J. R. Hockett, and H. L. Bergman. 1990*a*. Aluminum and acid toxicity to two strains of brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences **47**:1641–1648.

Ingersoll, C. G., D. R. Mount, D. D. Gulley, T. W. La Point, and H. L. Bergman. 1990*b*. Effects of pH, aluminum, and calcium on survival and growth of eggs and fry of brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences **47**:1580–1592.

Jassby, A. D., J. E. Reuter, R. P. Axler, C. R. Goldman, and S. H. Hackley. 1994. Atmospheric deposition of nitrogen and phosphorus in the annual nutrient load of Lake Tahoe. Water Resources Research **30**:2207–2216.

Jaworski, N. A., P. M. Groffman, A. A. Keller, and J. C. Prager. 1992. A watershed nitrogen and phosphorus balance: the Upper Potomac River basin. Estuaries **15**:83–95.

Jaworski, N. A., R. W. Howarth, and L. J. Hetling. 1997. Atmospheric deposition of nitrogen oxides onto the landscape contributes to coastal eutrophication in the northeast United States. Environmental Science and Technology **31**: 1995–2004.

Jeffries, D. S. 1995. A preliminary assessment of nitrogen-based fresh water acidification in southeastern Canada. Water, Air and Soil Pollution **85**:433–438.

Johnson, D. W. 1979. Some nitrogen fractions in two forest soils and their changes in response to urea fertilization. Northwest Science **53**:22–32.

———. 1992. Nitrogen retention in forest soils. Journal of Environmental Quality **21**:1–12.

Johnson, D. W., and S. E. Lindberg, editors. 1992. Atmospheric deposition and forest nutrient cycling. Ecological Studies 91. Springer-Verlag, New York, New York, USA.

Johnson, D. W., H. Van Miegroet, S. E. Lindberg, R. B. Harrison, and D. E. Todd. 1991. Nutrient cycling in red spruce forests of the Great Smoky Mountains. Canadian Journal of Forest Research **21**:769–787.

Johnson, D. W., R. F. Walker, and J. T. Ball. 1995. Lessons from lysimeters: soil N release from disturbance compromises controlled environment study. Ecological Applications **5**:395–400.

Jorgensen, J. R. 1967. Fractionation of nitrogen in three forest soils. Soil Science Society of America Proceedings **31**:707–708.

Joslin, J. D., J. M. Kelly, and H. Van Miegroet. 1992. Soil chemistry and nutrition of North American spruce-fir stands: evidence for recent change. Journal of Environmental Quality **21**:12–30.

Joslin, J. D., and M. H. Wolfe. 1992. Red spruce soil chemistry and root distribution across a cloud water deposition gradient. Canadian Journal of Forest Research **22**:893–904.

Joslin, J. D., and M. H. Wolfe. 1993. Temperature increase accelerates nitrate release from high-elevation red spruce soils. Canadian Journal of Forest Research **23**:756–759.

Joslin, J. D., and M. H. Wolfe. 1994. Foliar deficiencies of mature Southern Appalachian red spruce determined from fertilizer trials. Soil Science Society of America Journal **58**:1572–1579.

Kahl, J. S., S. A. Norton, I. J. Fernandez, K. J. Nadelhoffer, C. T. Driscoll, and J. D. Aber. 1993. Experimental inducement of nitrogen saturation at the watershed scale. Environmental Science and Technology **27**:565–568.

Kauppi, P. E., K. Mielikäinen, and K. Kuusela. 1992. Biomass and carbon budget of European forests, 1971 to 1990. Science **256**:70–74.

Kaye, J. P., and S. C. Hart. 1997. Competition for nitrogen between plants and soil microorganisms. Trends in Ecology and Evolution **12**:139–143.

Keeney, D. R., and J. M. Bremner. 1966. Determination and isotope-ratio analysis of different forms of nitrogen in soils: 4. Exchangeable ammonium, nitrate and nitrite by direct-distillation methods. Soil Science Society of America Proceedings **30**:583–587.

Kelly, J. M. 1988. Annual elemental input/output estimates for two forested watersheds in eastern Tennessee. Journal of Environmental Quality **17**:463–468.

Kiefer, J. W., and M. E. Fenn. 1997. Using vector analysis to assess nitrogen status of ponderosa and Jeffrey pine along deposition gradients in forests of southern California. Forest Ecology and Management **94**:47–59.

Kimmins, J. P. 1997. Forest ecology, a foundation for sustainable management. Second edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

Kincheloe, J. W., G. A. Wedemeyer, and D. L. Koch. 1979. Tolerance of developing salmonid eggs and fry to nitrate exposure. Bulletin of Environmental Contamination and Toxicology **23**:575–578.

Klemmedson, J. O., and B. J. Wienhold. 1992. Nitrogen mineralization in soils of a chaparral watershed in Arizona. Soil Science Society of America Journal **56**:1629–1634.

Koerselman, W., and A. F. M. Meuleman. 1996. The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. Journal of Applied Ecology **33**:1441–1450.

Koopmans, C. J., A. Tietema, and A. W. Boxman. 1996. The fate of ^{15}N enriched throughfall in two coniferous forest stands at different nitrogen deposition levels. Biogeochemistry **34**:19–44.

Kuyper, T. W. 1994. Fungal species diversity and forest ecosystem functioning in The Netherlands. Pages 99–122 *in* T. J. B. Boyle and C. E. B. Boyle, editors. Biodiversity, temperate ecosystems, and global change. NATO ASI Series I. Global environmental change. Volume 20. Springer-Verlag, Berlin, Germany.

Lajtha, K., B. Seely, and I. Valiela. 1995. Retention and leaching losses of atmospherically-derived nitrogen in the aggrading coastal watershed of Waquoit Bay, MA. Biogeochemistry **28**:33–54.

Langford, A. O., and F. C. Fehsenfeld. 1992. Natural vegetation as a source or sink for atmospheric ammonia: a case study. Science **255**:581–583.

Lawrence, G. B., M. B. David, and W. C. Shortle. 1995. A new mechanism of calcium loss in forest-floor soils. Nature **378**:162–165.

Lee, J. A., S. J. Woodin, and M. C. Press. 1986. Nitrogen assimilation in an ecological context. Pages 331–346 *in* H. Lambers, J. J. Neeteson and I. Stulen, editors. Fundamental ecological and agricultural aspects of nitrogen metabolism in higher plants. Martinus Nijhoff, Dordrecht, The Netherlands.

Lemly, A. D., and R. J. F. Smith. 1987. Effects of chronic exposure to acidified water on chemoreception of feeding stimuli in fathead minnows (*Pimephales promelas*): mech-

anisms and ecological implications. Environmental Toxicology and Chemistry **6**:225–238.

Li, C. Y., H. B. Massicote, and L. V. H. Moore. 1992. Nitrogen-fixing *Bacillus* sp. associated with Douglas-fir tuberculate ectomycorrhizae. Plant and Soil **140**:35–40.

Likens, G. E., F. H. Bormann, N. M. Johnson, D. W. Fisher, and R. S. Pierce. 1970. Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook Watershed Ecosystem. Ecological Monographs **40**:23–47.

Likens, G. E., F. H. Bormann, R. S. Pierce, and W. A. Reiners. 1978. Recovery of a deforested ecosystem. Science **199**: 492–496.

Likens, G. E., C. T. Driscoll, and D. C. Buso. 1996. Long-term effects of acid rain: response and recovery of a forest ecosystem. Science **272**:244–246.

Lindberg, S. E., M. Bredemeier, D. A. Schaefer, and L. Qi. 1990. Atmospheric concentrations and deposition of nitrogen and major ions in conifer forests in the United States and Federal Republic of Germany. Atmospheric Environment **24A**:2207–2220.

Lundborg, A. 1997. Reducing the nitrogen load: whole-tree harvesting—a literature review. Ambio **26**:387–393.

Lövblad, G., M. Amann, B. Andersen, M. Hovmand, S. Joffre, and U. Pedersen. 1992. Deposition of sulfur and nitrogen in the Nordic countries: present and future. Ambio **21**:339–347.

Lowrance, R. 1992. Groundwater nitrate and denitrification in a coastal plain riparian forest. Journal of Environmental Quality **21**:401–405.

Lowrance, R., R. Todd, J. Rail, Jr., R. Leonard, and L. Asmussen. 1984. Riparian forests as nutrient filters in agricultural watersheds. BioScience **34**:374–377.

Lynch, J. A., J. W. Grimm, and V. C. Bowersox. 1995. Trends in precipitation chemistry in the United States: a national perspective, 1980–1992. Atmospheric Environment **29**: 1231–1246.

Magill, A. H., J. D. Aber, J. J. Hendricks, R. D. Bowden, J. M. Melillo, and P. A. Steudler. 1997. Biogeochemical response of forest ecosystems to simulated chronic nitrogen deposition. Ecological Applications **7**:402–415.

Magill, A. H., M. R. Downs, K. J. Nadelhoffer, R. A. Hallett, and J. D. Aber. 1996. Forest ecosystem response to four years of chronic nitrate and sulfate additions at Bear Brooks Watershed, Maine, USA. Forest Ecology and Management **84**:29–37.

Magnuson, J. J., J. P. Baker, and E. J. Rahel. 1984. A critical assessment of effects of acidification on fisheries in North America. Philosophical Transactions of the Royal Society of London **B305**:501–516.

Majdi, H., and J. Bergholm. 1995. Effects of enhanced supplies of nitrogen and sulphur on rhizosphere and soil chemistry in a Norway spruce stand in SW Sweden. Water, Air and Soil Pollution **85**:1777–1782.

Marschner, B., K. Stahr, and M. Renger. 1989. Potential hazards of lime application in a damaged pine forest ecosystem in Berlin, Germany. Water, Air and Soil Pollution **48**:45–57.

Martikainen, P. J. 1984. Nitrification in two coniferous forest soils after different fertilization treatments. Soil Biology and Biochemistry **16**:577–582.

———. 1996. Microbial processes in boreal forest soils as affected by forest management practices and atmospheric stress. Pages 195–232 *in* G. Stotzky and J.-M. Bollag, editors. Soil biochemistry. Volume 9. Marcel Dekker, New York, New York, USA.

Matson, P. A., and P. M. Vitousek. 1990. Ecosystem approach to a global nitrous oxide budget. BioScience **40**:667–672.

Matzner, E., and D. Murach. 1995. Soil changes induced by air pollutant deposition and their implication for forests in central Europe. Water, Air and Soil Pollution **85**:63–76.

McNulty, S. G., and J. D. Aber. 1993. Effects of chronic nitrogen additions on nitrogen cycling in a high-elevation spruce-fir stand. Canadian Journal of Forest Research **23**: 1252–1263.

McNulty, S. G., J. D. Aber, and R. D. Boone. 1991. Spatial changes in forest floor and foliar chemistry of spruce-fir forests across New England. Biogeochemistry **14**:13–29.

McNulty, S. G., J. D. Aber, T. M. McLellan, and S. M. Katt. 1990. Nitrogen cycling in high elevation forests of the northeastern US in relation to nitrogen deposition. Ambio **19**:38–40.

McNulty, S. G., J. D. Aber, and S. D. Newman. 1996. Nitrogen saturation in a high elevation spruce-fir stand. Forest Ecology and Management **84**:109–121.

Mead, D. J., and W. L. Pritchett. 1975. Fertilizer movement in a slash pine ecosystem. II. N distribution after two growing seasons. Plant and Soil **43**:467–478.

Melillo, J. M., J. D. Aber, and J. F. Muratore. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology **63**:621–626.

Melillo, J. M., J. D. Aber, A. E. Linkins, A. Ricca, B. Fry, and K. J. Nadelhoffer. 1989. Carbon and nitrogen dynamics along the decay continuum: plant litter to soil organic matter. Plant and Soil **115**:189–198.

Melin, J., H. Nömmik, U. Lohm, and J. Flower-Ellis. 1983. Fertilizer nitrogen budget in a Scots pine ecosystem attained by using root-isolated plots and ^{15}N tracer technique. Plant and Soil **74**:249–263.

Miller, E. K., J. D. Blum, and A. J. Friedland. 1993. Determination of soil exchangeable-cation loss and weathering rates using Sr isotopes. Nature **362**:438–441.

Miller, H. G., J. D. Miller, and O. J. L. Pauline. 1976. Effect of nitrogen supply on nutrient uptake in Corsican pine. Journal of Applied Ecology **13**:955–966.

Miller, R. E., P. R. Barker, C. E. Peterson, and S. R. Webster. 1986. Using nitrogen fertilizers in management of coastal Douglas-fir. I. Regional trends of response. Pages 290–303 *in* C. D. Oliver, D. P. Hanley, and J. A. Johnson, editors. Douglas-fir: stand management for the future. College of Forest Resources, University of Washington, Seattle, Washington, USA.

Mitchell, M. J., C. T. Driscoll, J. S. Kahl, G. E. Likens, P. S. Murdoch, and L. H. Pardo. 1996*a*. Climatic control of nitrate loss from forested watersheds in the northeast United States. Environmental Science and Technology **30**: 2609–2612.

Mitchell, M. J., D. J. Raynal, and C. T. Driscoll. 1996*b*. Biogeochemistry of a forested watershed in the central Adirondack mountains: temporal changes and mass balances. Water, Air and Soil Pollution **88**:355–369.

Mohren, G. M. J., J. Van Den Burg, and F. W. Burger. 1986. Phosphorus deficiency induced by nitrogen input in Douglas fir in The Netherlands. Plant and Soil **95**:191–200.

Mortland, M. M., and A. R. Wolcott. 1965. Sorption of inorganic nitrogen compounds by soil materials. Pages 150–197 *in* W. V. Bartholomew and F. E. Clark, editors. Soil nitrogen. Agronomy 10. American Society of Agronomy, Madison, Wisconsin, USA.

Mosier, A., D. Schimel, D. D. Valentine, K. D. Bronson, and W. Parton. 1991. Methane and nitrous oxide fluxes in native, fertilized and cultivated grasslands. Nature **350**:330–332.

Mugasha, A. G., and D. J. Pluth. 1994. Distribution and recovery of ^{15}N-urea in a tamarack/black spruce mixed stand on a drained minerotrophic peatland. Forest Ecology and Management **68**:353–363.

Murdoch, P. S., and J. L. Stoddard. 1992. The role of nitrate in the acidification of streams in the Catskill Mountains of New York. Water Resources Research **28**:2707–2720.

NAPAP. 1993. National Acid Precipitation Assessment Pro-

gram. 1992 Integrated Assessment Report. National Acid Precipitation Assessment Program, Washington, D.C., USA.

Nadelhoffer, K. J., J. D. Aber, M. R. Downs, B. Fry, and J. M. Melillo. 1993. Biological sinks for nitrogen additions to a forested catchment. Pages 22–44 *in* K. Lajtha, and R. Michener, editors. Stable isotope studies in ecology and environmental science. Blackwell, Oxford, UK.

Nadelhoffer, K. J., J. D. Aber, and J. M. Melillo. 1983. Leaf-litter production and soil organic matter dynamics along a nitrogen-availability gradient in southern Wisconsin (USA). Canadian Journal of Forest Research **13**:12–21.

Nadelhoffer, K. J., J. D. Aber, and J. M. Melillo. 1985. Fine roots, net primary production, and soil nitrogen availability: a new hypothesis. Ecology **66**:1377–1390.

Nadelhoffer, K. J., M. Downs, B. Fry, J. D. Aber, A. H. Magill, and J. M. Melillo. 1995. The fate of ^{15}N-labeled nitrate additions to a northern hardwood forest in eastern Maine, USA. Oecologia **103**:292–301.

Näsholm, T., A. Nordin, A.-B. Edfast, and P. Högberg. 1997. Identification of coniferous forests with incipient nitrogen saturation through analysis of arginine and nitrogen-15 abundance of trees. Journal of Environmental Quality **26**: 302–309.

Nilsson, L.-O. 1995. Forest biogeochemistry interactions among greenhouse gases and N deposition. Water, Air and Soil Pollution **85**:1557–1562.

Nilsson, L.-O., and K. Wiklund. 1995. Indirect effects of N and S deposition on a Norway spruce ecosystem: an update of findings within the Skogaby project. Water, Air and Soil Pollution **85**:1613–1622.

Nixon, S. W. 1990. Marine eutrophication: a growing international problem. Ambio **19**:101.

———. 1995. Coastal marine eutrophication: a definition, social causes, and future concerns. Ophelia **41**:199–219.

Nohrstedt, H.-O., U. Sikström, E. Ring, T. Näsholm, P. Högberg, and T. Persson. 1996. Nitrate in soil water in three Norway spruce stands in southwest Sweden as related to N-deposition and soil, stand, and foliage properties. Canadian Journal of Forest Research **26**:836–848.

Nömmik, H. 1965. Ammonium fixation and other reactions involving a nonenzymatic immobilization of mineral nitrogen in soil. Pages 198–257 *in* W. V. Bartholomew and F. E. Clark, editors. Soil nitrogen. Agronomy 10. American Society of Agronomy, Madison, Wisconsin, USA.

Nömmik, H., and B. Popovic. 1971. Recovery and vertical distribution of ^{15}N labelled fertilizer nitrogen in forest soil. Studia Forestalia Suecica **92**.

Nömmik, H., and K. Vahtras. 1982. Retention and fixation of ammonium and ammonia in soils. Pages 123–172 *in* F. J. Stevensen, J. M. Bremner, R. D. Hauck, and D. R. Keeney, editors. Nitrogen in agricultural soils. Agronomy 22. American Society of Agronomy, Madison, Wisconsin, USA.

Norton, S. A., J. S. Kahl, I. J. Fernandez, L. E. Rustad, J. P. Scofield, and T. A. Haines. 1994. Response of the West Bear Brook Watershed, Maine, USA, to the addition of $(NH_4)_2SO_4$: 3-year results. Forest Ecology and Management **68**:61–73.

Officer, C. B., R. B. Biggs, J. Taft, L. E. Cronin, M. A. Tyler, and W. R. Boynton. 1984. Chesapeake Bay anoxia: origin, development, and significance. Science **223**:22–27.

Paerl, H. W. 1995. Coastal eutrophication in relation to atmospheric nitrogen deposition: current perspectives. Ophelia **41**:237–259.

Paul, E. A., and F. E. Clark. 1989. Soil microbiology and biochemistry. Academic Press, New York, New York, USA.

Peet, R. K. 1992. Community structure and ecosystem function. Pages 103–151 *in* D. L. Glenn-Lewis, R. K. Peet, and T. T. Veblen, editors. Plant succession: theory and prediction. Chapman and Hall, London, UK.

Perry, D. A., et al. 1991. Biological feedbacks to climate change: terrestrial ecosystems as sinks and sources of carbon and nitrogen. Northwest Environmental Journal **7**:203–232.

Peterjohn, W. T., M. B. Adams, and F. S. Gilliam. 1996. Symptoms of nitrogen saturation in two central Appalachian hardwood forest ecosystems. Biogeochemistry **35**: 507–522.

Peterjohn, W. T., and D. L. Correll. 1984. Nutrient dynamics in an agricultural watershed: observations on the role of a riparian forest. Ecology **65**:1466–1475.

Pietikäinen, J., and H. Fritze. 1995. Clear-cutting and prescribed burning in coniferous forest: comparison of effects on soil fungal and total microbial biomass, respiration activity and nitrification. Soil Biology and Biochemistry **27**: 101–109.

Powers, R. F. 1990. Nitrogen mineralization along an altitudinal gradient: interactions of soil temperature, moisture, and substrate quality. Forest Ecology and Management **30**: 19–29.

Prescott, C. E. 1995. Does nitrogen availability control rates of litter decomposition in forests? Plant and Soil **168–169**: 83–88.

Prescott, C. E., L. P. Coward, G. F. Weetman, and S. P. Gessel. 1993. Effects of repeated nitrogen fertilization on the ericacious shrub, salal (*Gaultheria shallon*), in two coastal Douglas-fir forests. Forest Ecology and Management **61**: 45–60.

Preston, C. M., and D. J. Mead. 1994. Growth response and recovery of ^{15}N-fertilizer one and eight growing seasons after application to lodgepole pine in British Columbia. Forest Ecology and Management **65**:219–229.

Price, K. S., D. A. Flemer, J. L. Taft, G. B. Mackiern, W. Nehlsen, R. B. Biggs, N. H. Burger, and D. A. Blaylock. 1985. Nutrient enrichment of Chesapeake Bay and its impact on the habitat of striped bass: a speculative hypothesis. Transactions of the American Fisheries Society **114**:97–106.

Puckett, L. J. 1995. Identifying the major sources of nutrient water pollution. Environmental Science and Technology **29**:408–414.

Radwan, M. A., J. S. Shumway, D. S. DeBell, and J. M. Kraft. 1991. Variance in response of pole-size trees and seedlings of Douglas-fir and western hemlock to nitrogen and phosphorus fertilizers. Canadian Journal of Forest Research **21**:1431–1438.

Raison, R. J., P. K. Khanna, M. J. Connell, and R. A. Falkner. 1990. Effects of water availability and fertilization on nitrogen cycling in a stand of *Pinus radiata*. Forest Ecology and Management **30**:31–43.

Raison, R. J., P. K. Khanna, and P. V. Woods. 1985. Mechanisms of element transfer to the atmosphere during vegetation fires. Canadian Journal of Forest Research **15**:132–140.

Rao, A. C., J. L. Smith, R. I. Papendick, and J. F. Parr. 1991. Influence of added nitrogen interactions in estimating recovery efficiency of labeled nitrogen. Soil Science Society of America Journal **55**:1616–1621.

Rastetter, E. B., M. G. Ryan, G. R. Shaver, J. M. Melillo, K. J. Nadelhoffer, J. E. Hobbie, and J. D. Aber. 1991. A general biogeochemical model describing the responses of the C and N cycles in terrestrial ecosystems to changes in CO_2, climate, and N deposition. Tree Physiology **9**:101–126.

Raynal, D. J., J. D. Joslin, F. C. Thorton, M. Schaedle, and G. S. Henderson. 1990. Sensitivity of tree seedlings to aluminum. III. Red spruce and loblolly pine. Journal of Environmental Quality **19**:180–187.

Reynolds, B., S. J. Ormerod, and A. S. Gee. 1994. Spatial patterns in stream nitrate concentrations in upland Wales in relation to catchment forest cover and forest age. Environmental Pollution **84**:27–33.

Richter, D. D., D. W. Johnson, and K. H. Dai. 1992. Cation exchange and Al mobilization in soils. Pages 341–377 *in* D. W. Johnson and S. E. Lindberg, editors. Atmospheric deposition and forest nutrient cycling. Ecological Studies 91. Springer-Verlag, New York, New York, USA.

Riggan, P. J., R. N. Lockwood, P. M. Jacks, C. G. Colver, F. Weirich, L. F. DeBano, and J. A. Brass. 1994. Effects of fire severity on nitrate mobilization in watersheds subject to chronic atmospheric deposition. Environmental Science and Technology **28**:369–375.

Riggan, P. J., R. N. Lockwood, and E. N. Lopez. 1985. Deposition and processing of airborne nitrogen pollutants in Mediterranean-type ecosystems of southern California. Environmental Science and Technology **19**:781–789.

Risser, P. G. 1995. The status of the science examining ecotones. Bioscience **45**:318–325.

Rosén, K., and A. Lundmark-Thelin. 1987. Increased nitrogen leaching under piles of slash—a consequence of modern forest harvesting techniques. Scandinavian Journal of Forest Research **2**:21–29.

Rothstein, D. E., D. R. Zak, and K. S. Pregitzer. 1996. Nitrate deposition in northern hardwood forests and the nitrogen metabolism of *Acer saccharum* marsh. Oecologia **108**:338–344.

Rustad, L. E., I. J. Fernandez, M. B. David, M. J. Mitchell, K. J. Nadelhoffer, and R. B. Fuller. 1996. Experimental soil acidification and recovery at the Bear Brook Watershed in Maine. Soil Science Society of America Journal **60**: 1933–1943.

Schimel, J. P., and M. K. Firestone. 1989. Nitrogen incorporation and flow through a coniferous forest soil profile. Soil Science Society of America Journal **53**:779–784.

Schulze, E.-D. 1989. Air pollution and forest decline in a spruce (*Picea abies*) forest. Science **244**:776–783.

Shaver, G. R., W. D. Billings, F. S. Chapin III, A. E. Giblin, K. J. Nadelhoffer, W. C. Oechel, and E. B. Rastetter. 1992. Global change and the carbon balance of arctic ecosystems. BioScience **42**:433–441.

Shortle, W. C., and K. T. Smith. 1988. Aluminum-induced calcium deficiency syndrome in declining red spruce. Science **240**:239–240.

Sievering, H., D. Rusch, and L. Marquez. 1996. Nitric acid, particulate nitrate and ammonium in the continental free troposphere: nitrogen deposition to an alpine tundra ecosystem. Atmospheric Environment **30**:2527–2537.

Silsbee, D. G., and G. L. Larson. 1982. Water quality of streams in the Great Smoky Mountains National Park. Hydrobiologia **89**:97–115.

Sitaula, B. K., L. R. Bakken, and G. Abrahamsen. 1995*a*. CH_4 uptake by temperate forest soil: effect on N input and soil acidification. Soil Biology and Biochemistry **27**:871–880.

Sitaula, B. K., L. R. Bakken, and G. Abrahamsen. 1995*b*. N-fertilization and soil acidification effects on N_2O and CO_2 emission from temperate pine forest soil. Soil Biology and Biochemistry **27**:1401–1408.

Sollins, P., C. C. Grier, F. M. McCorison, K. Cromack, Jr., R. Fogel, and R. L. Fredriksen. 1980. The internal element cycles of an old-growth Douglas-fir ecosystem in western Oregon. Ecological Monographs **50**:261–285.

Staaf, H., and B. A. Olsson. 1994. Effects of slash removal and stump harvesting on soil water chemistry in a clear-cutting in SW Sweden. Scandinavian Journal of Forest Research **9**:305–310.

Stams, A. J. M., and I. J. L. Schipholt. 1990. Nitrate accumulation in leaves of vegetation of a forested ecosystem receiving high amounts of atmospheric ammonium sulfate. Plant and Soil **125**:143–145.

Stark, J. M., and S. C. Hart. 1996. High rates of nitrification and nitrate turnover in undisturbed coniferous forests. Nature **385**:61–64.

Stednick, J. D. 1981. Hydrochemical balance of an alpine watershed in southeast Alaska. Arctic and Alpine Research **13**:431–438.

Steudler, P. A., R. D. Bowden, J. M. Melillo, and J. D. Aber. 1989. Influence of nitrogen fertilization on methane uptake in temperate forest soils. Nature **341**:314–316.

Stevens, P. A., A. F. Harrison, H. E. Jones, T. G. Williams, and S. Hughes. 1993. Nitrate leaching from a Sitka spruce plantation and the effect of fertilisation with phosphorus and potassium. Forest Ecology and Management **58**:233–247.

Stevens, P. A., and M. Hornung. 1990. Effect of harvest intensity and ground flora establishment on inorganic-N leaching from a Sitka spruce plantation in north Wales, UK. Biogeochemistry **10**:53–65.

Stevenson, F. J. 1982. Nitrogen—organic forms. Pages 625–641 *in* A. L. Page, R. H. Miller, and D. R. Keeney, editors. Methods of soil analysis. Part 2. Chemical and microbiological properties. Agronomy 9. Second edition. American Society of Agronomy and Soil Science Society of America, Madison, Wisconsin, USA.

Stoddard, J. L. 1994. Long-term changes in watershed retention of nitrogen: its causes and aquatic consequences. Pages 223–284 *in* L. A. Baker, editor. Environmental chemistry of lakes and reservoirs. Advances in Chemistry Series Number 237. American Chemical Society, Washington, D.C., USA.

Stoddard, J. L., and P. S. Murdoch. 1991. Catskill Mountains. Pages 237–271 *in* D. F. Charles, editor. Acidic deposition and aquatic ecosystems. Springer-Verlag, New York, New York, USA.

Stottlemyer, R. 1992. Nitrogen mineralization and streamwater chemistry, Rock Creek Watershed, Denali National Park, Alaska, USA. Artic and Alpine Research **24**:291–303.

Stottlemyer, R., and C. A. Troendle. 1995. Surface water chemistry and chemical budgets, alpine and subalpine watersheds, Fraser Experimental Forest, Colorado. Pages 321–327 *in* K. A. Tonnessen, M. W. Williams, and M. Tranter, editors. Proceedings: Biogeochemistry of Seasonally Snow-covered Catchments. XXI Assembly of the International Union of Geodesy and Geophysics, Boulder, Colorado, USA.

Sutton, M. A., C. E. R. Pitcairn, and D. Fowler. 1993. The exchange of ammonia between the atmosphere and plant communities. Advances in Ecological Research **24**:301–393.

Swank, W. T. 1988. Stream chemistry responses to disturbance. Pages 339–357 *in* W. T. Swank and D. A. Crossley, Jr., editors. Forest hydrology and ecology at Coweeta. Ecological Studies 66. Springer-Verlag, New York, USA.

Swift, M. J., O. W. Heal, and J. M. Anderson. 1979. Decomposition in terrestrial ecosystems. Studies in ecology. Volume 5. Blackwell Scientific, Oxford, UK.

Tamm, C. O., A. Aronsson, and B. Popvic. 1995. Nitrogen saturation in a long-term forest experiment with annual additions of nitrogen. Water, Air and Soil Pollution **85**: 1683–1688.

Termorshuizen, A. J. 1993. The influence of nitrogen fertilisers on ectomycorrhizas and their fungal carpophores in young stands of *Pinus sylvestris*. Forest Ecology and Management **57**:179–189.

Tiedemann, A. R., T. M. Quigley, and T. D. Anderson. 1988. Effects of timber harvest on stream chemistry and dissolved

nutrient losses in northeastern Oregon. Forest Science **34**: 344–358.

Ulrich, B. 1983. A concept of forest ecosystem stability and of acid deposition as driving force for destabilization. Pages 1–29 *in* B. Ulrich and J. Pankrath, editors. Effects of accumulation of air pollutants in forest ecosystems. D. Reidel, Dordrecht, The Netherlands.

Van Dijk, H. F. G., and J. G. M. Roelofs. 1988. Effects of excessive ammonium deposition on the nutritional status and condition of pine needles. Physiologia Plantarum **73**: 494–501.

Van Miegroet, H., and D. W. Cole. 1984. The impact of nitrification on soil acidification and cation leaching in a red alder forest. Journal of Environmental Quality **13**:586–590.

Van Miegroet, H., D. W. Cole, and N. W. Foster. 1992*a*. Nitrogen distribution and cycling. Pages 178–196 *in* D. W. Johnson and S. E. Lindberg, editors. Atmospheric deposition and forest nutrient cycling, Ecological Studies 91. Springer-Verlag, New York, USA.

Van Miegroet, H., D. W. Cole, and D. W. Johnson. 1990. Impact of forest floor C/N changes and soil N on nitrification in four forest soils. Canadian Journal of Forest Research **20**:1012–1019.

Van Miegroet, H., and D. W. Johnson. 1993. Nitrate dynamics in forest soils. Pages 75–97 *in* T. P. Burt, A. L. Heathwaite, and S. T. Trudgill, editors. Nitrate: processes, patterns and management. John Wiley and Sons, New York, New York, USA.

Van Miegroet, H., G. M. Lovett, and D. W. Cole. 1992*b*. Nitrogen chemistry, deposition, and cycling in forests: summary and conclusions. Pages 202–207 *in* D. W. Johnson and S. E. Lindberg, editors. Atmospheric deposition and forest nutrient cycling, Ecological Studies 91. Springer-Verlag, New York, New York, USA.

Verhoeven, J. T. A., W. Koerselman, and A. F. M. Meuleman. 1996. Nitrogen- or phosphorus-limited growth in herbaceous, wet vegetation: relations with atmospheric inputs and management regimes. Trends in Ecology and Evolution **11**:494–497.

Vitousek, P. M., J. D. Aber, R. W. Howarth, G. E. Likens, P. A. Matson, D. W. Schindler, W. H. Schlesinger, and D. G. Tilman. 1997*a*. Human alteration of the global nitrogen cycle: sources and consequences. Ecological Applications **7**:737–750.

Vitousek, P. M., and J. M. Melillo. 1979. Nitrate losses from disturbed forests: patterns and mechanisms. Forest Science **25**:605–619.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997*b*. Human domination of earth's ecosystems. Science **277**:494–499.

Vitousek, P. M., and W. A. Reiners. 1975. Ecosystem succession and nutrient retention: a hypothesis. BioScience **25**: 376–381.

Vought, L. B.-M., J. Dahl, C. L. Pedersen, and J. O. Lacoursière. 1994. Nutrient retention in riparian ecotones. Ambio **23**:342–348.

Wang, J., and L. R. Bakken. 1997. Competition for nitrogen during mineralization of plant residues in soil: microbial response to C and N availability. Soil Biology and Biochemistry **29**:163–170.

Waring, R. H. 1987. Nitrate pollution: a particular danger to boreal and subalpine coniferous forests. Pages 93–105 *in* T. Fujimori and M. Kimura, editors. Human impacts and management of mountain forests. Forestry and Forest Products Research Institute, Ibaraki, Japan.

Weathers, K. C., et al. 1988. Chemical composition of cloud water from ten sites in North America. Environmental Science and Technology **22**:1018–1026.

Wedin, D. A., and D. Tilman. 1996. Influence of nitrogen loading and species composition on the carbon balance of grasslands. Science **274**:1720–1723.

Wigington, P. J. Jr., D. R. DeWalle, P. S. Murdoch, W. A. Kretser, H. A. Simonin, J. Van Sickle, and J. P. Baker. 1996. Episodic acidification of small streams in the northeastern United States: ionic controls of episodes. Ecological Applications **6**:389–407.

Williams, E. J., and F. C. Fehsenfeld. 1991. Measurement of soil nitrogen oxide emissions at three North American ecosystems. Journal of Geophysical Research **96**:1033–1042.

Williams, M. W., J. S. Baron, N. Caine, R. Sommerfeld, and R. Sanford, Jr. 1996*a*. Nitrogen saturation in the Rocky Mountains. Environmental Science and Technology **30**: 640–646.

Williams, M. W., P. D. Brooks, A. Mosier, and K. A. Tonnessen. 1996*b*. Mineral nitrogen transformations in and under seasonal snow in a high-elevation catchment in the Rocky Mountains, United States. Water Resources Research **32**:3161–3171.

Wright, R. F., and A. Tietema. 1995. Ecosystem response to 9 years of nitrogen addition at Sogndal, Norway. Forest Ecology and Management **71**:133–142.

Wright, R. F., and N. van Breemen. 1995. The NITREX project: an introduction. Forest Ecology and Management **71**:1–5.

Young, J. R., E. C. Ellis, and G. M. Hidy. 1988. Deposition of air-borne acidifiers in the western environment. Journal of Environmental Quality **17**:1–26.

Zak, D. R., P. M. Groffman, K. S. Pregitzer, S. Christensen, and J. M. Tiedje. 1990. The vernal dam: plant-microbe competition for nitrogen in northern hardwood forests. Ecology **71**:651–656.

Zhen, R. G., and R. A. Leigh. 1990. Nitrate accumulation by wheat (*Triticum aestivum*) in relation to growth and tissue N concentrations. Pages 17–20 *in* M. L. van Beusichem, editor. Plant nutrition: physiology and applications. Kluwer Academic, Norwell, Massachusetts, USA.

Zinke, P. J. 1980. Influence of chronic air pollution on mineral cycling in forests. Pages 88–99 *in* P. R. Miller, editor. Proceedings of the Symposium on Effects of Air Pollutants on Mediterranean and Temperate Forest Ecosystems. Riverside, California, 22–27 June 1980. USDA Forest Service General Technical Report **PSW-43**.

Zischke, J. A., J. W. Arthur, K. J. Nordlie, R. O. Hermanutz, D. A. Standen, and T. P. Henry. 1983. Acidification effects on macroinvertebrates and fathead minnows (*Pimephales promelas*) in outdoor experimental channels. Water Research **17**:47–63.

Zöttl, H. 1960. Methodische Untersuchungen zur Bestimmung der Mineralstickstoffnachlieferung des Waldbodens. Forstwissenschaftliches Centralblatt **79**:72–90.

Zöttl, H. W. 1990. Remarks on the effects of nitrogen deposition to forest ecosystems. Plant and Soil **128**:83–89.